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Middle American Lizards of the Genus Ameiva (Teiidae) with Emphasis on Geographic Variation

By

Arthur C. Echternacht

UNIVERSITY OF KANSAS
LAWRENCE 1971

December 14, 1971

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University of Kansas
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Middle American Lizards of the Genus *Ameiva* (Teiidae) with Emphasis on Geographic Variation

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Lawrence
1971

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CONTENTS

INTRODUCTION 4

ACKNOWLEDGMENTS 5

MATERIALS AND METHODS 6

Characters 6

Statistical Procedures 11

Sexual Dimorphism 12

Sources of Specimens Examined 12

SYSTEMATIC ACCOUNT OF THE SPECIES 13

KEY TO THE MIDDLE AMERICAN SPECIES OF *AMEIVA* 13

Ameiva ameiva (Linnaeus) 14

Ameiva leptophrys Cope 20

Ameiva festiva (Lichtenstein and Von Martens) 26

Ameiva quadrilineata (Hallowell) 34

Ameiva undulata (Wiegmann) 40

Ameiva chaitzami Stuart 59

DISCUSSION 63

INTERSPECIFIC RELATIONSHIPS 63

INTERSPECIFIC PATTERNS IN GEOGRAPHIC VARIATION 64

HISTORY OF *AMEIVA* IN MIDDLE AMERICA 67

SUMMARY 71

RESUMEN 72

APPENDIX A: SUMMARY OF STATISTICS 75

APPENDIX B: SPECIMENS EXAMINED 76

LITERATURE CITED 83

INTRODUCTION

In their revision of the Mexican species of *Ameiva*, Smith and Laufe (1946) prefaced their comments with the remark that interest in these species had "been rising to a crescendo whose peak surely could soon be anticipated." Little could they have foreseen the surge of interest, both taxonomic and ecological, that the entire genus has enjoyed over the past five years. This attention has been precipitated by the realization that *Ameiva*, by virtue of its wide distribution in the Neotropical Realm and the extremes of variation exhibited by its species, is especially well suited for ecological, biogeographical, and evolutionary studies. Coupled with this has been the discovery that some species of *Ameiva* act as vectors for disease-causing organisms actually or potentially dangerous to humans (for example, see Schneider, 1965).

There are three natural geographic groupings of *Ameiva*: those found on the various islands of the Caribbean, those on the continent of South America, and those from Middle America (México and Central America). Taxonomic studies of the Caribbean *Ameiva* have been conducted by Baskin and Williams (1966), Heatwole and Torres (1967), Schwartz (1965, 1967, 1968), Schwartz and Klinikowski (1966), and Schwartz and McCoy (1970). Very little recent work has been done on the *Ameiva* of South America; the only study is that of Peters (1964) on the Ecuadorian species. No recent comprehensive taxonomic studies have been made of the Middle American species, although Stuart (1942) and Smith and Laufe (1946) contributed to our knowledge of certain species. The most recent revision of the entire genus is that of Barbour and Noble (1915). Their conclusions concerning the Middle American species of *Ameiva* were based on examination of only 41 specimens, a situation which largely masked the remarkable degree of geographic variation exhibited by some of the species. It is the purpose of this study to present an analysis of the geographic variation in each of the Middle American species of *Ameiva* as well as to summarize known information on the biology and ecology of these lizards.

Some persons will look upon the present work as justification for the recognition of subspecies of Middle American *Ameiva*. The controversy over subspecies has been debated extensively and heatedly elsewhere (Wilson and Brown, 1953; Peters, *et al.*, 1954; Smith and White, 1956; Savage and Heyer, 1967; Smith, 1967; and others), and I will not dwell on it here other than to state my conviction that a thorough description of geographic variation may make unwarranted and often undesirable the arbitrary nomenclatural fragmentation of highly variable species.

There is a growing body of evidence indicating the congeneric status of *Ameiva* and *Cnemidophorus*. Vanzolini and Valencia (1965), Estes (1969), and Gorman (1970) demonstrated the closeness of the relationship and discussed the difficulties encountered in trying to diagnose the two genera on the basis of known characters. Gorman (1970:240), however, was hesitant to make a decisive statement on the matter when he commented: "The similarity of karyotypes between *Ameiva* and the southernmost *Cnemidophorus* species group does not necessarily demonstrate close relationship, but there seem to be no characters that clearly separate the two genera." I believe that the argument will not be resolved until increased knowledge of South American *Ameiva*, especially the perplexing *A. lacertoides*, is available. The condition of the base of the tongue (free and heart-shaped in *Cnemidophorus*, sheathed in *Ameiva*) has been considered to be diagnostic (Burt,

1931), but *A. lacertoides* has a *Cnemidophorus*-like tongue (Vanzolini and Valencia, 1965; personal observation). I prefer not to comment on the issue, but instead await the completion of relevant investigations by Richard Estes, George C. Gorman, William P. MacLean III, and William Presch.

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During the course of this study, I have built up a huge debt of gratitude to many people who have provided assistance in one way or another. I have probably taxed the patience of a number of museum curators, curatorial assistants, and collectors with requests for the loan of large numbers of specimens and locality or ecological data on specific specimens. I especially acknowledge the following: Kraig K. Adler, the late Doris M. Cochran, James R. Dixon, William E. Duellman, Henry S. Fitch, George Foley, Jean Guibé, Günther Peters, Robert F. Inger, Daniel A. Janzen, John M. Legler, Charles H. Lowe, Edmond V. Malnate, Hymen Marx, John R. Meyer, Charles W. Myers, Thomas Olechowski, James A. Peters, Douglas C. Robinson, Richard D. Sage, Jay M. Savage, Norman J. Scott, Hobart M. Smith, Dorothy M. Smith, A. G. Stimson, L. C. Stuart, Stephen G. Tilley, Donald W. Tinkle, Robert G. Tuck, Jaime Villa, Ernest E. Williams, John W. Wright and Richard G. Zweifel.

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I have had the benefit of a great deal of constructive criticism and advice from my colleagues at the University of Kansas Museum of Natural History. William E. Duellman has been a constant source of encouragement, and his patience with me has, at times, been remarkable. He, along with Henry S. Fitch and Ronald L. McGregor, have reviewed this manuscript. Donald R. Clark, Ko Ko Gyi, John D. Lynch, Russell J. Hall, Charles W. Myers, E. H. Taylor and Linda Trueb have been willing to discuss special problems as they arose, and their help is gratefully acknowledged.

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E. Raymond Hall, Philip S. Humphrey, and William E. Duellman of the University of Kansas Museum of Natural History have allowed me free access to the collections and facilities of the museum. The Panamanian collections made by Duellman and Charles W. Myers have been especially useful. Field work was financed in part by National Science Foundation Summer Fellowships for Graduate Teaching Assistants (1965 and 1966) and by travel grants and traineeships provided by the Committee for Systematics and Evolutionary Biology from funds granted by the National Science Foundation (Grant No. GB-4446X) to the University of Kansas, Dr. William A. Clemens and Dr. George W. Byers, principal investigators (1966-1968). A grant-in-aid from the Society of the Sigma Xi provided funds for illustrations, which were executed by Mrs. Susann Jacobshagen. Computer-time was made available by the University of Kansas and Boston University Computer Centers.

To my wife Sandra, I owe my greatest thanks. She has been a constant source of encouragement and support and has proven to be an able assistant in both field and laboratory. She has cheerfully endured the many inconveniences experienced by the families of graduate students, and, with the realization that the debt can never be repaid, I dedicate this work to her.

MATERIALS AND METHODS

This study is based on the examination of over 3000 specimens of *Ameiva*, 2848 of which were examined in detail with respect to morphology, color and pattern. Samples were drawn from throughout the ranges of *Ameiva festiva*, *A. leptophrys*, *A. quadrilineata*, *A. undulata*, and *A. chaitzami*. Only Panamanian specimens of *Ameiva ameiva* were examined, because to include specimens from throughout the range of the species would have necessitated examination of material from South America, where inadequate geographic representation of samples would have made any conclusions more than usually speculative. *Ameiva ameiva* will be included in a projected study of South American members of the genus which will be completed only after field work necessary for the accumulation of samples representative of the entire South American range of the species is possible. South American samples of *Ameiva festiva* have been included in the present study because the range of the species is primarily in Central America.

For purposes of statistical analysis, I attempted to amass samples of at least 30 specimens (ideally 15 males and 15 females) from relatively restricted localities. This attempt was only partially successful in that, with the exceptions of Guatemala and parts of México, large series of *Ameiva* from single localities are not available. Of necessity, samples of ten or more have been used; for characters showing sexual dimorphism (Table 1), the samples were still smaller. Greater success was achieved in accumulation of samples representative of the ranges of the species, although lack of collections from critical areas in Panamá has precluded exact statements of variation in *A. ameiva* and, especially, *A. leptophrys*.

In each of the species accounts, a short synonymy, statement of distribution, diagnosis, and description are followed by an extensive discussion of infraspecific geographic variation, ecological notes, and general remarks. A discussion of interspecific relationships and the history of the genus *Ameiva* in Middle America follows the species accounts.

Characters

In the interests of standardization of methods, a definition of each of the characters analyzed in this study follows. Unless stated otherwise, characters are defined in the same manner as by Smith (1946). An asterisk (*) indicates a character analyzed for geographic variation by Power's (1970) modification of Gabriel's (1964) Sums of Squares Simultaneous Test Procedure (STP). Interpretation of the results of STP analysis is summarized in the section on statistical procedures. It will be noted that certain characters were not taken for some species, whereas in other instances a character was taken but not analyzed by the STP method.

Snout-Vent Length (SVL).—The distance, to the nearest millimeter, from the tip of the snout to the anterior margin of the vent. Maximum observed values for males and females of each species are given. Collections seem to be biased in favor of larger (male) individuals. Measurements were taken with a flexible plastic rule.

Head Length.—The distance to the nearest 0.1 millimeter from the tip of the snout to the posterior surface of the quadrate bone. The latter point was found by piercing the tympanum with one tip of the dial calipers and hooking the tip behind the bone. That the quadrate was, in fact, the bone encountered was verified by x-ray photography.

**Supralabials.*—The total number of supralabials on both sides of the head. The posterior supralabial is herein defined as the last enlarged scale in contact with both the lip and a subocular scale (Fig. 1a).

*Infralabials.—The total number of infralabials on both sides of the head. The posterior infralabial is determined by the point at which the masseter muscle and associated membranes pass from the lower to the upper jaw.

*Terminal Sublabials.—This character was noted for *Ameiva festiva* only. Stuart (1943:21) utilized the number of terminal sublabials to distinguish *A. festiva festiva* from *A. f. edwardsi*. I counted the sublabials present in the position of the two terminal sublabials of a "typical" *A. f. festiva*, totaling the numbers obtained for both sides of the head. By this method, a "typical" *A. f. festiva* (*sensu* Stuart) has four, whereas *A. f. edwardsi* has six or more.

*Supraoculars.—The total number of supraoculars on both sides of the head. Supraoculars are numbered from front to back (3a-c, Fig. 1b); there are three or four on each side of most specimens of *Ameiva* from Middle America.

*Loreals.—The total number of loreals on both sides of the head. If more than one loreal is present on one side of the head, the second is smaller and usually located at the angle formed by the contact between supralabials and suborbitals anterior to the eye (3, Fig. 1a). Occasionally, there are two loreals about equal in size, one dorsal to the other. If a third scale is present in the area encompassed by the loreal(s), it is counted as a third loreal only if it is one-half the size of the smaller of the two other loreals or larger.

**Degree of Circumorbital Granule Contact With the Frontal* (COF).—The degree of contact by the circumorbital granular scales with the frontal was coded for purposes of statistical analysis as follows: 1) circumorbital granules not in contact with frontal-frontoparietal suture (Fig. 1b), 2) circumorbital granules in contact with frontal-frontoparietal suture, but not extending past it (Fig. 1c), 3) circumorbital granules extending forward past the frontal-frontoparietal suture (Fig. 1d). The coded values obtained for both sides of the head were totaled. Thus, the lowest possible value for a given specimen is two; the highest is six.

**Circumorbital Pattern* (COP).—The position of the anteriormost circumorbital granule relative to the supraocular scales was coded as follows: 1) granules extending to the level of the middle of the first supraocular scale, 2) granules extending to the level of the suture between the first and second supraocular scales, 3) granules reaching the level of the middle of the second supraocular scale (Fig. 1d), 4) granules extending to the level of the suture between the second and third supraocular scales (Fig. 1c), 5) granules extending to the level of the middle of the third supraocular scale (Fig. 1b), 6) granules extending to the level of the suture between the third and fourth supraocular scales or, if there is no fourth supraocular, granules not reaching the level of the middle of the third supraocular, 7) granules extending to the middle of the fourth supraocular scale. Coded values for both sides of the head were totaled for analysis.

**Extent of the Double Row of Granules Between the Supraocular and Superciliary Scales* (SO-SC).—This character was coded as follows: 1) single row of granules between the superciliary and supraocular series (Fig. 1d), 2) double row of granules extending forward to the level of the middle of the third supraocular scale, 3) double row of granules extending forward to the suture between the second and third supraocular scales, 4) double row of granules extending forward to the level of the middle of the second supraocular (Fig. 1c), 5) double row of granules completely separating the superciliary scales from the second and third supraocular scales (Fig. 1b). Coded values for both sides of the head were totaled for analysis.

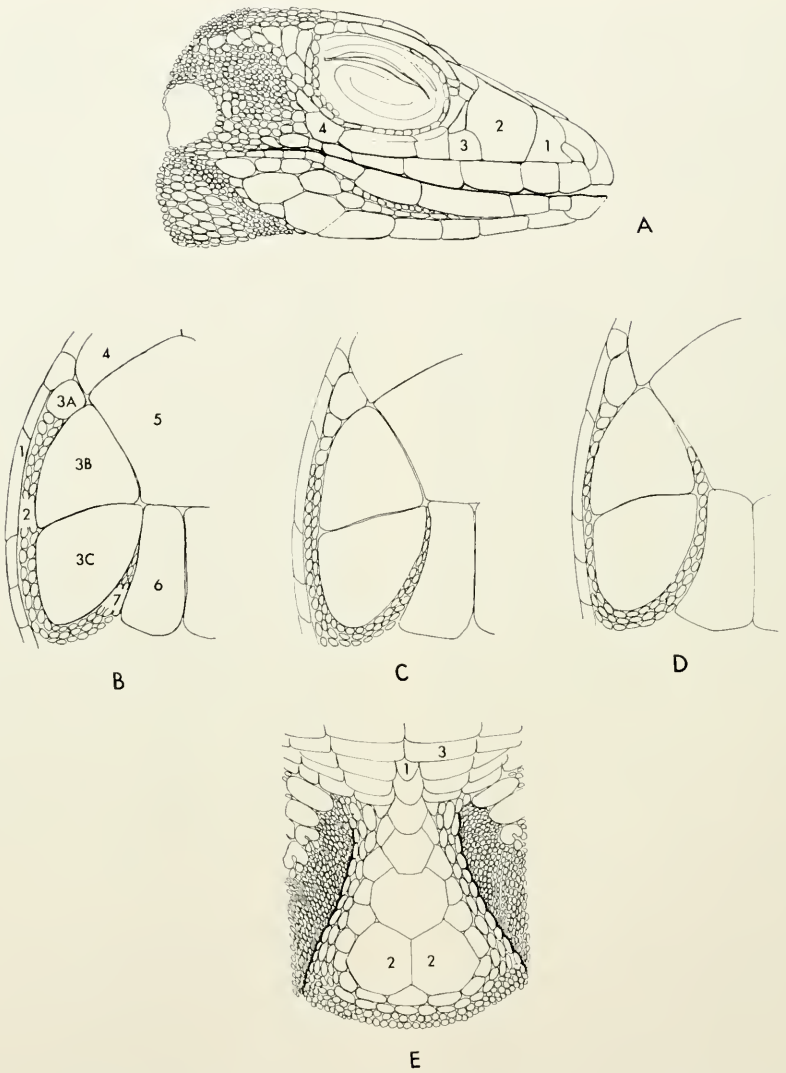

FIG. 1. Details of head and preanal scutellation of *Ameiva*. (A) Lateral view of head: 1.—Postnasal; 2.—Anterior loreal; 3.—Posterior loreal; 4.—Suborbital scale in contact with posterior supralabial (small, rectangular scale below 4). (B, C, and D) Dorsal view of head, left supraorbital region: 1.—Superciliary series; 2.—Supraocular-superciliary granules; 3A, 3B, and 3C.—Anterior, middle and posterior supraocular scales, respectively; 4.—Prefrontal scale; 5.—Frontal scale; 6.—Frontoparietal scale; 7.—Circumorbital granules. (E) Preanal region: 1.—Anterior (1st) preanal scale; 2.—Posterior (last) preanal scale; 3.—Terminal row of ventral scutes.

Gular Scales.—The central gular scales are small and irregular in arrangement, large and irregular, or large and oriented longitudinally in the midline. Intermediate conditions exist, but most specimens can be assigned without difficulty. If enlarged midgular scales are present, the smaller scales around them may become gradually smaller toward the periphery of the gular region or may become gradually smaller laterally and anteriorly but abruptly

very small posteriorly. If the latter is true, the gular region is distinctly divided into pregular and postgular areas (see Fig. 5c, *A. leptophrys*).

Mesoptychial Scales.—The mesoptychial scales are small and irregular, continuous with the posterior gular scales, or they may form a band of abruptly enlarged scales across the throat.

**Granules Around the Body* (GAB).—The number of granules around the body was shown by Zweifel (1959) to be of diagnostic importance in distinguishing species of *Cnemidophorus*, and this character has been used extensively by students of that difficult genus. In most cases, the character has been given as "scales around midbody" (I believe the term "granules" to be more descriptive), but rarely is there a statement as to what "midbody" refers. This is important inasmuch as the character is intended to be a measure of granule size, and the granules vary in size over the length of the body. In this study, GAB counts were made starting at a point adjacent to the 15th transverse row of enlarged ventral scutes, the first transverse row of ventral scutes is taken as the first row extending entirely across the chest behind the gular fold.

**Paravertebral Granules* (PV).—The number of granules between, and including, the paravertebral stripes of *Ameiva leptophrys*, *quadrilineata*, *undulata*, and *chaitzami*.

**Vertebral Stripe* (VS).—The number of granules included within the vertebral light stripe of *Ameiva festiva*.

PV and VS counts were omitted for *A. ameiva* because the stripes are lacking or very faint on most adults of that species.

**PV/GAB Ratio.*—The ratio of paravertebral granules, as defined above, to granules around the body was calculated.

**Granules Occiput to Rump* (GOR).—The number of granular scales between the enlarged occipital scales and the large, keeled dorsal caudal scales was counted for all species. Although there is usually a high correlation between values obtained for this count and those for granules around the body (correlation coefficient=0.75 and 0.54 for males and females of *A. leptophrys*, respectively), GOR sometimes shows sexual dimorphism and occasionally is an easier and more accurate count than GAB. The latter is especially true in poorly preserved specimens that have been coiled or that have numerous folds in the skin of the flanks. With experience, neither GAB nor GOR counts are difficult or time-consuming to make, and error is not excessive (2-3% based on recounts of the same specimens). The most suitable technique for counting dorsal granules seems to be to use a fine insect pin as a pointer and marker while counting granules beneath a wide-field, binocular microscope. Ideally, the specimens should be slightly dry, since fluid between the granules results in glare and makes counting difficult.

**GAB/GOR Ratio.*—This ratio was calculated for all species.

Prebrachials.—The number of rows of prebrachials was noted.

Postbrachials.—The postbrachials are enlarged or not.

Preantebrachials.—The number of rows of preantebrachial scales was recorded.

Prefemoral Scales.—Prefemoral scales are defined herein as the large scales on the anterior and ventral surfaces of the upper hind leg as far back as the femoral pore series. Thus defined, prefemorals include the infrafemoral and prefemoral scales of Smith (1946:28). The number of rows was counted.

Infratibial Scales.—The number of rows of infratibial scales was counted.

The number of rows of preantebrachials, prebrachials, prefemorals and infratibials is variable throughout the length of the series on a single specimen. In many specimens, there is a greater number of scales medially than

proximally. This variation is discussed for each species.

**Femoral Pores.*—The number of femoral pores was recorded; counts given in the text and tables are for the total number of pores on both legs.

**Subdigital Lamellae.*—The number of subdigital lamellae on the anterior margin of the fourth (longest) toe of the left hind foot was recorded. The starting point for this count is the tubercule immediately proximal to the enlarged tubercule at the base of the first phalanx. If there is no tubercule in this position, the enlarged basal terminal is itself used as the starting point.

**Longitudinal Rows of Ventral Scutes.*—The number of rows of enlarged ventral scutes was counted between the gular fold and the first preanal scale, as defined below. The first row is the anteriormost row extending entirely across the chest posterior to the gular fold.

**Transverse Rows of Ventral Scutes.*—The number of transverse rows of ventral scutes was counted at the level of the 15th longitudinal row of ventrals. The outer row on each side is reduced in size in some specimens.

**Total Preanal Scales.*—The number of preanal scales from just posterior to the terminal row of longitudinal ventral scutes to the enlarged scale(s) preceding the vent were counted. The first preanal scale is usually single, lies between the proximal femoral pores of each leg, and is distinguished from the last row of ventrals by its unpaired condition (1, Fig. 1e). Smith and Laufe (1946:20) encountered difficulty in determining which preanal scale is terminal because the preanal scales occasionally grade in size into the granular scales immediately anterior to the vent. When in doubt as to which preanal or row of preanals is terminal, I have simply recorded the last row having three or fewer enlarged scales. In most cases, this is obviously the terminal row anyway. In those lizards with a single terminal preanal, the scales lateral to it are usually very much smaller and create no confusion as to whether or not they are part of the terminal preanal series.

**Terminal Preanal Scales.*—The number of scales in the terminal position in the preanal series was determined by the method outlined above (2, Fig. 1e).

**Scales Around the Tail* (SAT).—The number of scales around the tail was counted at the level of the 15th verticil of caudal scales; the first verticil was taken as that row of caudal scales which first completely encircles the tail posterior to the vent.

Various aspects of color and color pattern were noted on a sample-by-sample basis. Recurring pattern components noted were as follows:

Vertebral Stripe.—A narrow stripe originating on the snout or occiput and terminating on the tail unless completely or partially lost in adults.

Middorsal Field or Area.—A broad stripe, containing a vertebral stripe or not, originating on the occiput and terminating on the tail, bordered laterally by the dorsolateral light stripes, if present, or the dorsolateral dark field.

Dorsolateral Light Stripe.—A narrow, light-colored stripe originating on, or posterior to, the superciliary rows and terminating on the tail and which may be entirely or partially lost in adults.

Secondary Stripe.—A narrow, dark-colored stripe, the lateral border of which is the dorsolateral light stripe, if present, or the dorsolateral dark field and the medial border is the lighter part of the middorsal field in which it lies.

Dorsolateral Dark Field.—A dark, often black or dark brown, area bounded above by the dorsolateral light stripe, if present, or the middorsal field and below by the ventrolateral light stripe, if present, or the ventrolateral field; originating on the loreal scales,

terminating on the tail and interrupted by the eye; may be indistinct or lost in adults.

Ventrolateral Light Stripe.—A narrow, light-colored stripe originating at the posterior margin of the eye or posterodorsal margin of the ear and extending along the body to the groin, usually continuing behind the leg and slightly onto the tail.

Ventrolateral Field or Area.—Ventrolateral one-half or two-thirds of the flanks bordered above by the ventrolateral light stripe, if present, or the dorsolateral dark field and below by the enlarged ventral scutes; distinguished from the dorsolateral dark field by its generally lighter color; may contain irregularly arranged spots, blotches and/or bars or regularly spaced vertical bars.

Lateral Bars or Blotches.—Regular blotches in the dorsolateral dark field or bars on the flanks.

Head scutellation is extremely variable in *Ameiva*. This is especially evident in *Ameiva leptophrys* and, to a lesser extent, in *festiva* and *quadrilineata*. The supraoculars of specimens of *quadrilineata* from the Bocas del Toro region of Panamá are so fragmented as to preclude counting them. There may be three or four supraoculars per side in any of the Middle American species of *Ameiva*, and specimens of all species are known which have four on one side, three on the other. The number of supraoculars is thought to be sufficiently constant in *Cnemidophorus* that the number is used to distinguish species groups (Burt, 1931). The posterior dorsal head scales of *Ameiva leptophrys* (Fig. 7) and some *festiva* are variously fragmented, so that in extreme cases parietal scales are not recognizable, and the frontoparietals and frontal are only slightly less disrupted. It might seem that such variability in the posterior head scales of *Ameiva* renders them useless for taxonomic purposes, but it seems that the amount of variation is a useful taxonomic character. For example, the presence of small, irregular scales separating the interparietal from the parietals and frontoparietals can be used to distinguish *leptophrys* from other Middle American *Ameiva*.

Statistical Procedures

Statistical summaries of all species examined comprise Appendix A.

Power's (1970) modification of Gabriel's (1964; see Gabriel and Sokal, 1969) Sums of Squares Simultaneous Test Procedure (STP) provides a test of significance or non-significance of differences among sample means and is employed only after an overall analysis of variance demonstrates significant differences among the means. Samples are then ranked in decreasing order of their means and sums of squares calculated by sequentially adding means (beginning with the largest) until a maximal non-significant subset is delimited. The procedure is then repeated, deleting one or more of the larger means in the previously defined subset, until another maximal non-significant subset is described. This procedure is repeated until all samples have been included in at least one such subset. A constant probability level of 0.05 was used in the study, as recommended by Power (1970). Calculations were performed by the University of Kansas Computation Center on a GE-625 computer, and at Boston University on an IBM 360-40.

In addition to STP, a number of statistics were calculated for each species and each sample. Certain of these, along with the STP results, are summarized in the tables accompanying each species account. Information pertaining to the total number of femoral pores of Panamanian *Ameiva ameiva* will serve as an example for the interpretation of STP results (see Appendix A). The first column of numbers includes the locality code, keyed to the range map of Panamanian *A. ameiva* (Fig. 2). The localities are ordered in

TABLE 1.—Occurrence of sexual dimorphism among Middle American *Ameiva* as determined by STP analysis. A, *ameiva;* L, *leptophrys;* Q, *quadrilineata;* F, *festiva;* U, *undulata;* C, *chaitzami;* N, not tested.

Character	Species						Character	Species					
	A	L	Q	F	U	C		A	L	Q	F	U	C
Supralabials	−	+	−	+	+	−	PV/GAB	N	−	−	−	+	−
Infralabials	−	−	−	−	−	−	GOR	+	−	−	+	−	+
Supraoculars	−	−	−	−	−	−	GAB/GOR	+	−	+	−	+	−
COF values	+	−	−	−	−	−	SAT	−	−	+	−	+	−
COP values	−	−	−	−	−	−	Total Preanals	−	+	+	+	+	−
SO-SC values	N	−	N	N	−	−	Terminal Preanals	+	+	+	+	−	−
Loreals	N	−	N	N	−	−	Subdigital Lamellae	−	−	+	−	−	−
Sublabials	N	N	N	+	N	N	Trans. Rows of Ventrals	−	−	−	−	−	−
GAB	−	−	−	+	−	−	Long. Rows of Ventrals	−	−	−	−	−	−
PV	N	−	−	+	+	−	Femoral Pores	−	+	+	+	+	+

terms of the decreasing magnitude of their means, given in column two. Following the mean values are the standard deviation of the mean, sample size (in parentheses), and observed range. To the right of each block of statistics are the STP results, appearing as vertical lines. There are no STP results given if the overall analysis of variance indicated no significant differences among the sample means, and in these instances the samples are ordered by their locality numbers irrespective of their mean values. In the example, samples 6 and 5, with means of 35.0 and 34.1, respectively, form the first maximal nonsignificant subset and are so indicated by the left-most line. Localities 5, 7, 3, 2 and 1 constitute the second subset (middle line), and localities 7, 3, 2, 1 and 4 are the third (right line). The mean for locality 6 is significantly different from all other means, except that of locality 5 as indicated by the observation that the mean for locality 6 appears in no subsets containing means other than that of locality 5. Likewise, locality 5 is significantly different from locality 4. Localities 5 and 7 are not statistically different, although it would appear so if only the third subset were considered, but in this subset locality 5 was omitted from the comparison in order to allow other means into the subset at the lower end of the scale. Localities 5 and 7 are from the same statistical population, because they are both included in the second subset.

Statistical significance must be interpreted with caution. One cannot infer gene pool similarities from knowledge of a single character; for example, it would be improper to consider lizards from central México and Costa Rica as belonging to the same biological population, even if they are shown to belong to the same statistical population. It is well known that phenotypic expression of the genotype can be modified by environmental pressures and similarities, or differences in a particular character among samples from divergent localities simply may be an expression of this pressure on a relatively plastic genome.

Sexual Dimorphism

Presence or absence of sexual dimorphism for individual characters was determined by analysis of variance. This was done for each locality sample of *Ameiva festiva* and *undulata*, for all males against all females of *A. ameiva*, *chaitzami*, and *leptophrys*, and for Atlantic slope males versus Atlantic slope

females and Pacific slope males versus Pacific slope females of *quadrilineata*. If any sample as so defined was sevually dimorphic for a character, the entire If any sample as so defined was sexually dimorphic for that character for purposes of statistical analysis. Presence or absence of sexual dimorphism for most of the characters utilized in this study is indicated in Table 1.

Sources of Specimens Examined

A complete list of specimens examined, along with locality data for each, is included in Appendix B. The following abbreviations have been used in referring to individual specimens and indicate the museum or private collection in which the specimens are housed.

ANSP	Academy of Natural Sciences of Philadelphia
AMNH	American Museum of Natural History
ARP	A. R. Philips Collection (University of Arizona)
BMNH	British Museum (Natural History)
FMNH	Field Museum of Natural History
JRM	John R. Meyer (Private Collection)
LACM	Los Angeles County Museum
MCZ	Museum of Comparative Zoology
MNHN	Museum National d'Histoire Naturelle, Paris
RDS	Richard D. Sage (Private Collection)
TCWC	Texas Cooperative Wildlife Collection
USNM	United States National Museum
UCR	Universidad de Costa Rica
UCLA	University of California at Los Angeles (Specimens now housed in the Los Angeles County Museum)
UIMNH	University of Illinois Museum of Natural History
KU	University of Kansas Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USC(CRE)	University of Southern California (Costa Rican Expedition)
UU	University of Utah
ZMB	Zoologisches Museum, Berlin

SYSTEMATIC ACCOUNT OF THE SPECIES

I have recognized six species of *Ameiva* in Middle America. All of these are easily recognizable in the field by the experienced student, but are easily confused when dealing with preserved specimens. As is often the case, the species cannot be distinguished readily on the basis of single characters, and identification of preserved specimens can be difficult even if a suite of characters is used. The following artificial key should be used in conjunction with the tables in the analyses of geographic variation and with the descriptions of color and pattern variation. No attempt has been made to place the key into a phylogenetic framework. Fortunately, the situation is not so bad as that which caused Stuart (1955), in discussing his key to Guatemalan *Anolis*, to comment that ". . . the worker who knows what species he has before him should experience few difficulties in its use."

KEY TO THE MIDDLE AMERICAN SPECIES OF *AMEIVA*

1. Ten to twelve longitudinal rows of ventral scutes; mesoptychial scales subequal; adults spotted ..... *ameiva*

   Eight longitudinal rows of ventral scutes; transverse row of enlarged mesoptychial scales; principally striped 2

2. Posterior gular scales smaller than anterior gular scales 3

   Anterior and posterior gular scales subequal in size 4

3. Postnasal scales not in contact with prefrontals; lateral parietal and frontoparietal scales separated by one or more rows of small, irregular scales; midgular scales greatly enlarged, irregular in arrangement ..... *leptophrys*

   Postnasal scales in contact with prefrontals; parietal and frontoparietal

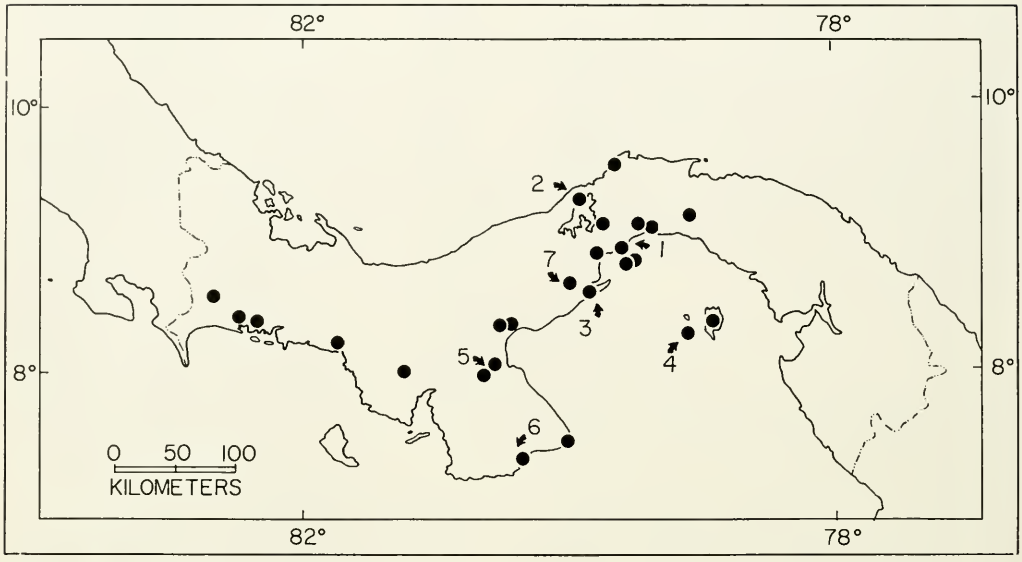

Fig. 2. Map showing locality records for *Ameiva ameiva* in Panamá. To avoid crowding of symbols, some localities have been omitted. Samples used in statistical analyses were (1) Vicinity of Panamá City, (2) Vicinity of Colón, (3) Vicinity of Nuevo Gorgona, (4) Isla San José, (5) Prov. Herrera, (6) Prov. Los Santos, and (7) Vicinity of Cerro Campana.

scales in contact; midgular scales slightly to moderately enlarged, irregular or in a single longitudinal row ..... *quadrilineata*

4. Midgular scales much enlarged, irregular in arrangement; narrow, light-colored vertebral stripe present except in large adults ..... *festiva*

   Midgular scales much enlarged, in longitudinal arrangement or not, moderately enlarged and irregular in arrangement; no vertebral stripe 5

5. Small (maximum observed SVL 85 mm for males, 75 mm for females); paravertebral stripe narrow (mean PV = 37.1); dorsolateral blotches in males fused to dorsolateral light stripe ..... *chaitzami*

   Moderately large (maximum observed SVL 129 mm for males, 111 mm for females); paravertebral stripe broad (mean PV = 47.4 for males, 46.4 for females); dorsolateral blotches in males, if present, do not fuse with dorsolateral light stripe ..... *undulata*

Ameiva ameiva (Linnaeus)

Lacerta ameiva Linnaeus, Systema naturae, ed. 12, 1:362, 1766.—America.

Cnemidophorus praesignis Baird and Girard, Proc. Acad. Nat. Sci. Philadelphia, 6:129, 1852 [Syntypes: USNM 5519 and UMMZ 3823, Chagres, Panamá; C. B. Adams, collector].

Ameiva praesignis—Cope, Proc. Acad. Nat. Sci. Philadelphia, 14:67, 1862.

Ameiva praesigna—Bocourt, Mission Scientifique au Méxique et dans l'Amerique Centrale; Études sur les reptiles, livr. 3, p. 265, pl. 20b, fig. 9-9d, 1874.

Ameiva surinamensis—Boulenger, Catalogue of the Lizards in the British Museum (Natural History), 2nd Ed., vol. 2, p. 352, 1885 (part). Günther, Biologia Centrali-Americana; Reptilia and Batrachia, p. 22, pl. 19, 1885 (part).

Ameiva ameiva praesignis—Barbour and Noble, Bull. Mus. Comp. Zool., 59(6):468, 1915. Dunn, Proc. Acad. Nat. Sci. Philadelphia, 92:113, 1940.

Distribution in Panamá.—Grasslands and savannas of the Pacific slopes near Chepo, Panamá, to David, Chiriquí, and in open areas across the Canal Zone to Colón and Portobelo, Colón, on the Atlantic side (Fig. 2).

Diagnosis.—*Ameiva ameiva* can be distinguished from all other Middle American *Ameiva* by the following combination of characters: Size large, maximum observed SVL 197 mm for males and 157 mm for females; mesoptychial scales small, irregular; scales around the tail more than 30; ventrals at midbody usually more than eight; supraoculars usually eight; color pattern in adult males emphasizes spots, rather than longitudinal stripes or lateral bars and blotches.

Description.—Maximum observed SVL 197 mm for males, 157 mm for females; 11-16 (12.9) supralabials; 8-12 (10.1) infralabials; 6-10 (8.0) supraoculars; COF values 2-6 (2.1), but note geographic variation discussed below; COP values 8-16 (10.6); nostril in prenasal-postnasal suture; prefrontals in contact with postnasals; loreals 2; GAB 128-204 (146.0), 204 an exceptional value—the second highest value recorded was 169; GOR 229-324 (287.8) for males, 225-394 (295.5) for females; GAB/GOR 0.45-0.68 (0.51) for males, 0.41-0.67 (0.49) for females; SAT 34-45 (39.5); total preanal scales 7-16 (10.8); terminal preanal scales 2-3 (2.4) for males, 2-3 (2.2) for females; one row of enlarged prebrachials with irregularly arranged accessory rows on either side; postbrachials slightly to moderately enlarged, irregularly arranged; preantebrachials enlarged, one (occasionally two) rows; prefemoral scales enlarged, in four or more rows; infratibial scales in three rows; femoral pores 25-41 (32.4); subdigital lamellae 26-36 (30.9); longitudinal rows of ventral scutes 28-33 (31.2); transverse rows of ventral scutes 6-12 (11.0); dorsal caudal scales weakly keeled. For details of scutellation see figure 3.

Color and Pattern in Alcohol.—Juvenile males: Top and upper half of side of head gray-green to brown with black markings immediately anterior to eye; lower one-half of head from eye to postnasal white; supralabials black above,

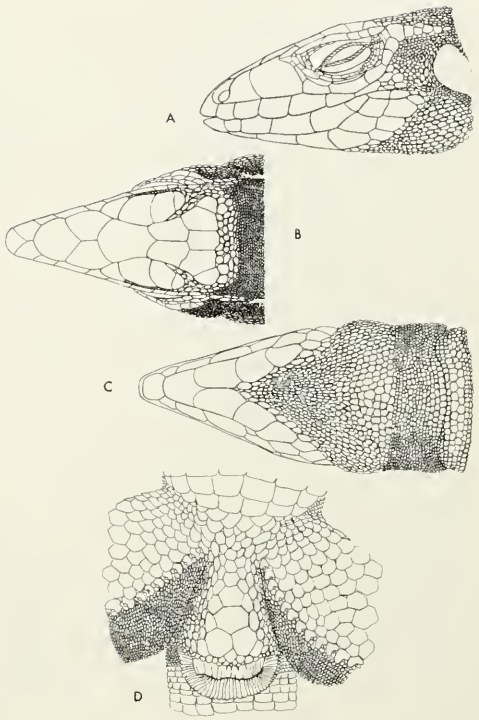

Fig. 3. Head and preanal scutellation of *Ameiva ameiva* from Panama (KU 108258): (A) Lateral view of head, (B) Dorsal view of head, (C) Ventral view of head. × 1.3. (D) Preanal region. × 2.

white below to lip; infralabials black below, white above to lip; chin and gular region white or cream with small, scattered flecks and often a transverse row of black flecks between larger median gulars and smaller posterior gulars; middorsal area between occiput and tail black or dark brown with brown or gray-green middorsal stripe, anterior one-fifth of which as broad as paravertebral field, gradually narrowing to a width of about 10 granules near base of tail and with irregular margins throughout; cream or gray-white paravertebral stripes from (and including) superciliary series well onto tail; dorsolateral dark stripe black with or without a brown median stripe and with many small, white or blue-white spots; lateral light stripe cream, originating at dorsoposterior margin of ear and extending

to point of insertion of hind leg and onto anterior surface of thigh, beginning again on posterior surface of thigh and extending well onto tail; area between lateral light stripe and ventral scutes black with small, white spots (some indistinct); venter white or cream medially with lateral scutes and (occasionally) chest marked with black flecks; dorsal surfaces of fore and hind limbs black with blue, blue-white or pale brown spots and blotches, this color and pattern grading to uniform cream or white ventrally with or without black flecks; pre- and postfemoral light stripes cream. Tail brown with black or blue-gray flecking above, flecks sometimes arranged to give the appearance of whorls; white dorsolateral stripe; sides black with white flecking; ventrolateral light stripe white, blending into white or cream ventral coloring; subcaudal area sometimes with black blotches; short, black postanal stripes extending from each corner of the vent.

Through ontogeny there is a gradual loss of stripes and an increased emphasis on spotting, so that in adult males the dorsal pattern is one of transverse rows of white or blue-white spots on a black background with indistinct gray-green or pale brown areas between the rows of spots (Fig. 4). Anteriorly, the pattern breaks down altogether, leaving only fine, light brown reticulations on a black background. This pattern carries over onto the dorsal surfaces of the forelimbs and the granules of the side of the head. The hind limbs become black with blue flecks, again sometimes arranged to give the appearance of whorls. Ventrally, the body, tail and hind limbs are blue; the chin, gular region and forelimbs white or cream with black flecks. In adult males the chin, gular region, and the forepart of the chest may be pale orange. Males from eastern Panamá retain a bright orange or reddish-tan vertebral stripe as adults.

Females: Juvenile females resemble juvenile males, but there is strong sexual dimorphism in adult color patterns (Fig. 4). Adult females retain longitudinal stripes, and spotting does not become as pronounced as in adult males. Adult females have brownish-white to white dorsolateral and lateral stripes bounded by black. Middorsally, there may be a remnant of the vertebral stripe (this is always true of specimens from eastern Panamá) with the remaining area mottled gray-green or brown on black with scattered white spots. A short cream stripe originating at the posteroventral corner of the ear and ending at the shoulder may be present. The dorsolateral dark stripe is black with white spots and may contain a diffuse, brown secondary stripe. Between the lateral light stripe and the enlarged ventral scutes there is a broad, light brown stripe. Some females have no spotting at all, the areas between the paravertebral and lateral light stripes appearing uniformly green or pale brown. All combinations of plain and spotted patterns in middorsal, dorsolateral and ventrolateral fields may be found.

Color and Pattern in Life.—The following description of color in life of *Ameiva ameiva* is quoted (with modifications to eliminate abbreviations) from the field notes of C. W. Myers and

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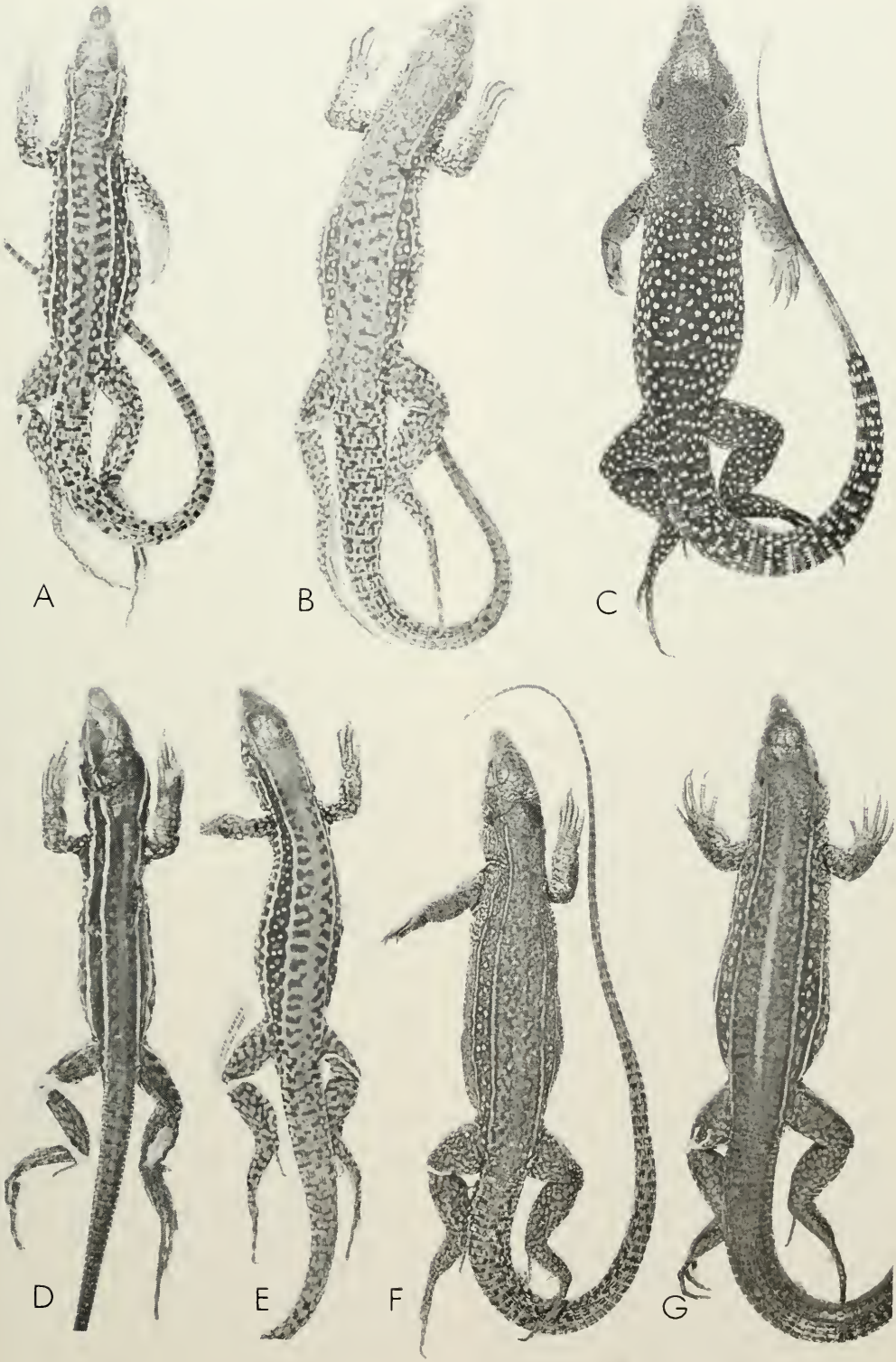
Fig. 4. Ontogenetic Change and Variation in Pattern of *Ameiva ameiva* from Panamá. Males: (A) KU 107521, SVL 68 mm, from Guánico, Los Santos Prov.; (B) KU 107542, 107 mm, from Pesé, Herrera Prov.; (C) KU 107532, 160 mm, from Guánico, Los Santos Prov. Females: (D) KU 76106, 45 mm, from S Slope Cerro Campana, Panamá Prov.; (E) KU 95546, 92 mm, from the Río Salado, Chiriquí Prov.; (F) KU 107524, 132 mm, from Guánico, Los Santos Prov.; (G) KU 108259, 150 mm, from Juan Mina, Chagres River, Canal Zone. Small males resemble small females as exemplified by KU 76106 (D above). KU 108259 (G above) is included to illustrate the presence of a well defined vertebral stripe in adult lizards from eastern Panamá (see text for discussion).


A
B
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pertains to specimens collected at Guánico Arriba, Los Santos, Panamá:

(KU 107521-3; juveniles) ". . . Middorsum brown with darker brown marks and bounded by pale yellow dorsolateral stripe. Sides rich brown or blackish brown, with pale tan dots, bordered below by a creamy stripe." (KU 107524-7; adult females) ". . . Dorsolateral and lateral stripes remain conspicuous, and the dorsum takes on a greenish tinge or not; a variable amount of tan to yellow dorsal spots. Throat light orange, and undersides of arms orange tinged to light dull red; rest of venter white in one and pale blue in the others; rear of the thighs white or pinkish white. Iris light brown." (KU 107528-31; adult males) ". . . Body stripes absent or inconspicuous and body with many conspicuous light spots which tend to be greenish yellow above and pale yellow on sides. Venter as in females but there seems to be a tendency for the colors, especially the orange, to be brighter (but the belly of one is bluish white). Iris light brown."

Geographic Variation.—Sample localities are indicated in figure 2. Of the characters analyzed by STP, the following show no among-sample statistical significance (ranges of sample means in parentheses): Total infralabials (9.8-10.2), total supraoculars (8.0-8.1), COF values for females (2.0), GOR (males, 282.5-295.8; females, 288.5-318.2), and GAB/GOR (males, 0.50-0.51; females, 0.47-0.50). As previously stated, *A. ameiva* from eastern Panamá differ from individuals from western Panamá in their retention of a distinct vertebral stripe as adults. Specimens collected west of a line between Penonomé, Coclé, and the mouth of the Río Estáncia, Coclé, lack the stripe as adults.

On the basis of STP results, the sample from Isla San José in the Bay of Panamá (Sample 4) can be distinguished from other samples in three characters (within sample ranges followed by sample means in parentheses): Total supralabials 14-15 (14.4), other samples 11-16 (12.3-12.8); COF values for males 2-6 (4.5), other samples 2 (2.0); COP values 8-12 (9.2), other samples 8-15 (10.0-12.0). Additionally, the Isla San José sample has the largest sample means for the following characters, although the sample does not differ statistically from mainland samples for these characters: total supraoculars, GAB, GOR for females, GAB/GOR for males, terminal preanals for females, and transverse rows of ventrals. The sample values were lowest among the localities compared for GAB/GOR for females, femoral pores, ventrals at midbody and COP values. With respect to the total number of supralabials, the significant difference between sample 4 and other samples is probably a function of the few large samples available for analysis. That inclusion of other samples in the comparison might alter the picture is suggested by values obtained for this character from small, mainland samples and from small samples from other islands in the Bay of Panamá. Values intermediate between that obtained for Isla San José and mainland samples used in STP analysis were obtained from Isla Taboga (mean = 13.0, n = 5); Río Mamoní, Panamá (13.6, 10); vicinity of Nata, Coclé (13.6, 5); Río Chorcha east of Chiriquí, Chiriquí (13.8, 5); and Isla San Miguel (14.0, 6). A sample of five specimens from Tres Puntas, Herrera, has a mean of 14.6, higher than that of the Isla San José sample for total number of supralabials.

Samples 5 and 6 from the Azuero Peninsula can be distinguished statistically as a unit from other samples for COP values, 12 (12.0) and 10-13 (11.9), respectively; other samples 8-15 (9.2-10.5). These samples possess the greatest (although not statistically significant) mean values for total number of femoral pores and number of subdigital lamellae.

On the mainland of Panamá, distinct

geographic trends are apparent only for the number of femoral pores, number of terminal preanals of males and COP values. All of these characters show increasing values from east to west. Values obtained for small samples not used in STP analysis indicate the same trends. Other characters demonstrate no geographic trends although certain localities differ from others statistically.

Ecological Notes.—Ameiva ameiva is characteristic of open areas in Panamá. It is common in the savannas of the lower Pacific slopes and in cleared areas across the Canal Zone. Cochran (1946) reported it in the same habitat on Isla San José. It has adapted well to the presence of man and is common in residential parts of Panamá City. Heatwole (1966) reported *A. ameiva* to be absent in the Darién Gap and noted that the Panamanian population of the species is disjunct from South American populations. He postulated that the species was once continuously distributed over the isthmus but that post-Columbian reforestation isolated the Panamanian population. Heatwole further demonstrated that *A. ameiva* is presently expanding its range eastward in Panamá by moving into areas recently cleared by man.

Remarks.—It is difficult to explain the presence of two geographically distinct color types (presence or absence of a reddish vertebral stripe in adults) of *Ameiva ameiva* in Panamá. Present environmental conditions are similar east and west of the Penonomé-Río Estáncia line. Bennett (1968) provided a clue to solution of the problem with his suggestion that the eruption of Volcán El Valle, which may have occurred during the Pleistocene (Terry, 1956), was an event of biogeographic importance. The ejecta from El Valle may have covered many square miles and could have divided the Panamanian population of *Ameiva ameiva* for sufficient time for divergence of color pattern to occur. Detailed ecological investigations of *A. ameiva* might yield information on this point, as well as on the origins of east-west clines for certain other characters, but no such studies have been undertaken. Even statistical studies aimed at correlating geographic variation in characters with environmental factors cannot be carried out until samples of adequate size for analysis can be accumulated from throughout the range of the species in Panamá. Taxonomic recognition of segments of the Panamanian population of *Ameiva ameiva* would be premature until analysis of character variation throughout the range of the species in South America can be completed.

Two specimens of *Ameiva surinamensis (=A. ameiva)* were listed by Boulenger (1885:353) as collected in Costa Rica by "Mr. Geale." There are no records at the British Museum that these lizards (BMNH 80.6.21.1-2) were collected by Geale himself, although the museum bought a number of specimens from him between 1866 and 1880 (Mr. A. F. Stimson, pers. comm.). The specimens are indeed *A. ameiva* and can be referred to the subspecies *praesignis* which ranges through northwestern Venezuela, northeastern Colombia and Panamá, but it is doubtful that they were collected in Costa Rica. Both specimens possess relatively well-defined middorsal stripes, suggesting that they may have come from eastern Panamá, if they were collected in Central America at all. There is presently no suitable habitat for *A. ameiva* in Costa Rica with the possible exception of the dry Guanacaste region where the species is not now known.

Barbour and Noble (1915) examined specimens of *Ameiva ameiva* ostensibly from Acapulco, México. Re-examination of the specimens (MCZ 2728 and 2730) confirms the identification, but the locality information is obviously erroneous.

Yunker and Radovsky (1966) and Brennan and Yunker (1966) reported

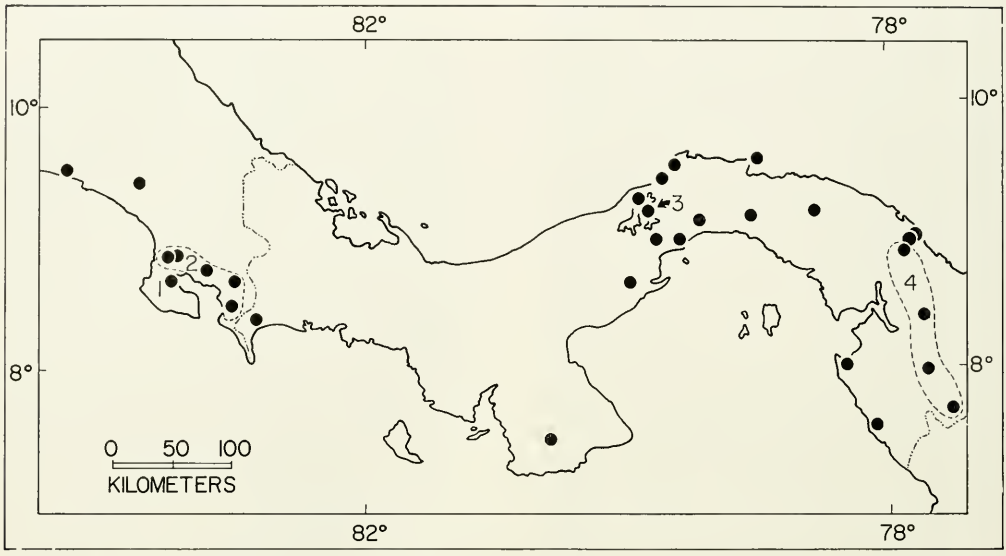


FIG. 5. Map showing locality records of *Ameiva leptophrys*. To avoid crowding of symbols, some localities have been omitted. Samples used in statistical analyses were (1) Osa Peninsula, Puntarenas Prov., Costa Rica, (2) Palmar-Golfito Region, Puntarenas Prov., Costa Rica, (3) Barro Colorado Island, Canal Zone, Panamá, and (4) Eastern Darién Prov., Panamá.

the acarinids *Draconysus belgicae* Yunker and Radovsky, *Eutrombicula alfreddugesi* (Oudemans) and *E. goeldi* (Oudemans) parasitic on *Ameiva bifrontata* from Panamá. Examination of the series of lizards from which these parasites were taken proves them to be *A. ameiva*.

Ameiva leptophrys Cope

Amiva leptophrys Cope, Proc. Amer. Phil. Soc., 31:341-342, 1893 [Holotype: Apparently lost; given by Cope as "No. 318." Type Locality: "Buenos Ayres" (=Buenos Aires, Puntarenas Prov., Costa Rica)].

Ameiva leptophrys—Dunn, Proc. Acad. Nat. Sci. Philadelphia, 92:114, 1940. Stuart, Proc. Biol. Soc. Washington, 55:146, 1942. Taylor, Univ. Kansas Sci. Bull., 38(1): 257-260, 1956.

Ameiva ruthveni Barbour and Noble, Bull. Mus. Comp. Zool., 59(6):471-473, 1915 [Holotype: MCZ 10927. Type Locality: near Panamá City. Collector: W. W. Brown, Jr.]. Burt and Burt, Trans. Acad. Sci. St. Louis, 28(1):53, 1933.

Ameiva festiva—Wettstein, Sitzungsb. Akad. Wiss. Wien, math.-naturw. Kl., Abt. I, 143. Bd., 1.u.2 Heft. p. 30, 1934 (part).

Distribution.—Forested areas of Pacific slopes from Parrita, Puntarenas Prov., and San Isidro del General, San José Prov., Costa Rica to Jaqué, Darién Prov., and the Río Mono, Darién Prov., within a few kilometers of the Colombian border in Panamá; across the Canal Zone and east along the Atlantic slopes at least as far as the Río Sasardi, San Blas Prov., Panamá (Fig. 5). The species probably occurs in extreme northwestern Colombia.

Diagnosis.—*Ameiva leptophrys* can be distinguished from its Middle American congeners by the following combination of characters: Separation of parietal and frontoparietal scales from the interparietal by one or more rows of small, irregular scales; abrupt reduction in size of small scales immediately posterior to the enlarged, median gular scales; large number of femoral pores (mean number for males, 49.1; females, 44.7); a transverse row of abruptly enlarged mesoptychial scales; eight longitudinal rows of ventral scutes; color pattern emphasizing longitudinal stripes rather than spotting, but lacking a light vertebral stripe.

Description.—Maximum observed

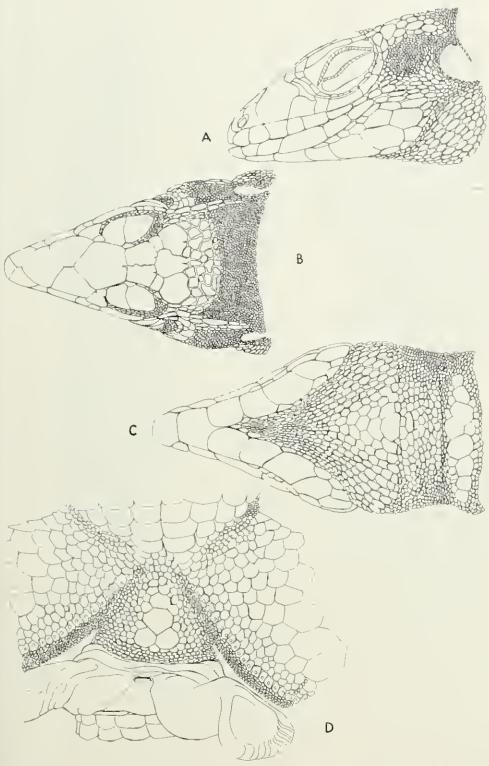


Fig. 6. Head and preanal scutellation of *Ameiva leptophrys*: (A) Lateral view of head, KU 96827, (B) Dorsal view of head, KU 96827, (C) Ventral view of head, KU 96827. × 1.2. (D) Preanal region, KU 96815. × 1.

SVL 133.0 for males, 129.0 for females; supralabials 11-15 (12.5) for males, 12-15 (12.7) for females; infralabials 10-12 (10.1); supraoculars 6-8 (6.2); COF values 2-6 (3.5); COP values 5-10 (8.1); SO-SC values 2-10 (5.9); loreals 2-6 (3.7); nostril in prenasal-postnasal suture; prefrontal usually not in contact with postnasal (96.3%, N = 136); GAB 127-182 (153.8); PV 28-63 (41.0); PV/GAB 0.19-0.35 (0.26); GOR 182-285 (235.6); GAB/GOR 0.54-0.74 (0.66); SAT 18-25 (21.0); total preanal Scales 4-10 (6.6) for males, 6-10 (8.1) for females; terminal preanal Scales 1-3 (2.1) for males, 1-3 (1.9) for females; one row of enlarged prebrachials; postbrachials not enlarged to moderately enlarged, irregularly arranged or in one or two rows; preantebrachials enlarged, in two rows proximally, one row distally; 3 (usually) or 4 rows of enlarged prefemoral scales; two rows of enlarged infratibials; femoral pores 42-61 (49.1) for males, 34-53 (44.7) for females; subdigital lamellae 24-35 (28.1); longitudinal rows of ventral scutes 26-31 (28.8); transverse rows of ventral scutes 8-10 (8.1). For details of scutellation see figure 6.

Individual variation in dorsal head scutellation is extreme (Fig. 7). There is no predictable pattern to scutellation posterior to the frontal, and even this scale may be divided. However, usually two frontoparietal and three parietal scales can be recognized. The degree of variation in posterior head scales is unequalled by other species of Middle American *Ameiva*, although it is approached in the closely related *A. festiva*.

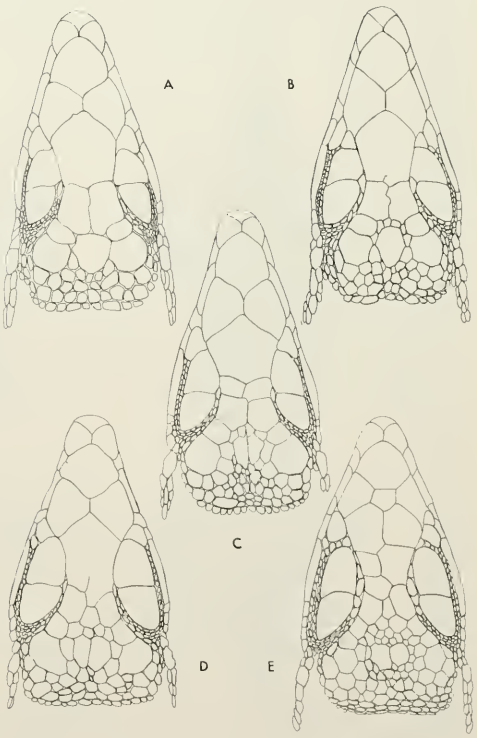


Fig. 7. Variation of dorsal head scutellation of *Ameiva leptophrys*. (A) KU 96820, × 2, (B) KU 96826, × 2.2, (C) KU 96814, × 2.3, (D) KU 95577, × 3.8, (E) KU 25641, × 4.1.

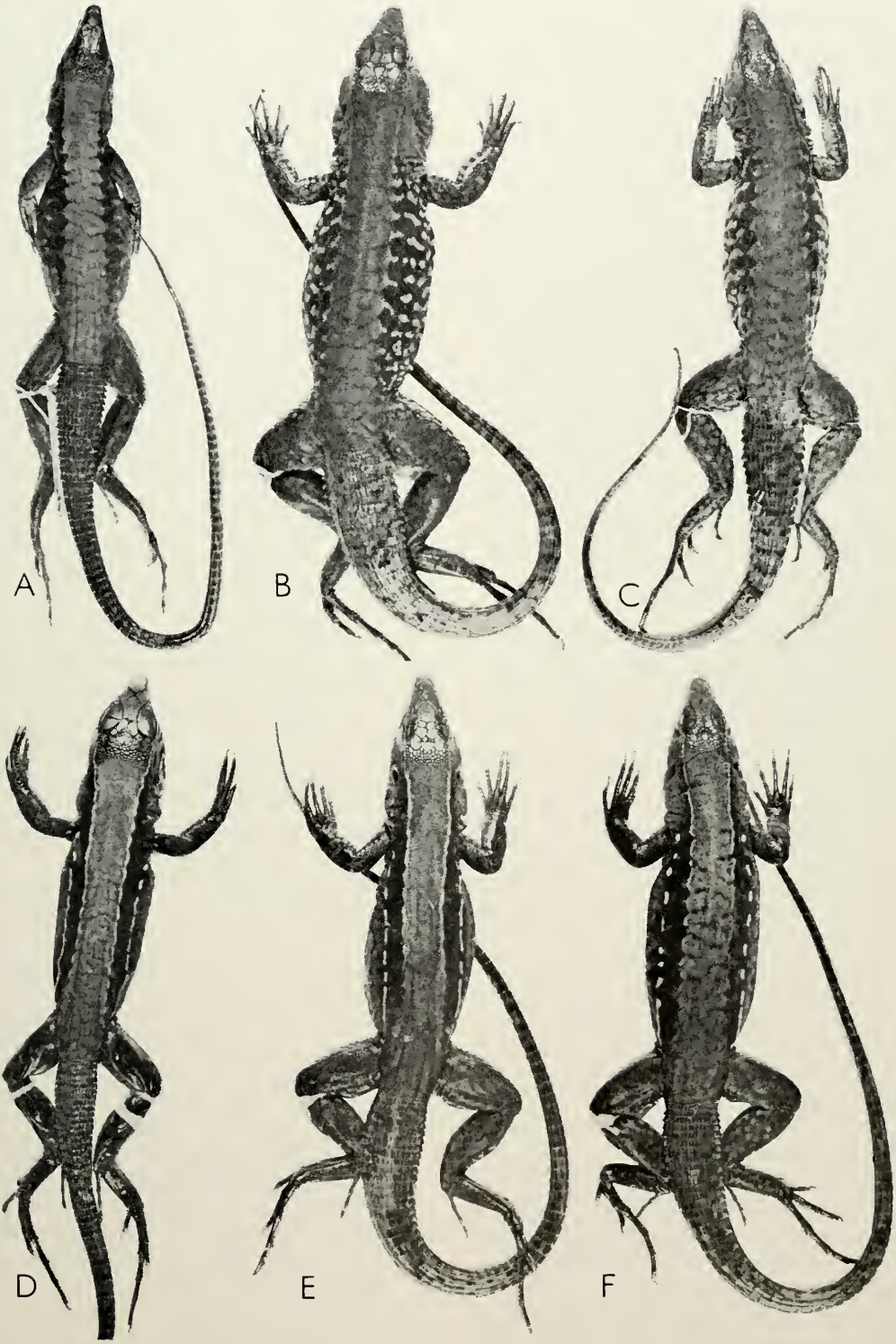
Color and Pattern in Alcohol.—Juvenile males: Top of head light brown; rostral and anterior part of frontonasal pearl-white with a slight greenish tinge; side of head dark brown above grading to gray-brown below; area between orbit and ear brown with darker brown postorbital bar dorsally; white crescent beneath and slightly behind eye; chin, infralabials, gular region and throat immaculate. Middorsal stripe broad, slightly irridescent, gray-brown, bordered laterally by white paravertebral stripes originating on superciliary scales and extending well onto tail; paravertebral stripes (and edges of middorsal stripe) undulating on posterior three-quarters of body; velvet-black dorsolateral stripe from above shoulder to insertion of hind legs, bordered below by broken white line originating on shoulder and extending to insertion of hind limbs and onto anterior surface of femur; area below this lateral light stripe brown, grading to gray-brown above ventral scutes. Venter immaculate. Dorsal surfaces of fore and hind limbs dark brown with lighter brown blotches, spots or mottling; no postfemoral light stripe; ventral surfaces of limbs immaculate to gray-white. Tail brown with black flecks above, brown laterally (below dorsolateral light stripe) blending to white or gray-white ventrally; short postanal white stripe bounded by brown below for about six scales, then joining white ventral pattern.

Through ontogeny (Fig. 8) the margins of the middorsal stripe become more undulating and the paravertebral stripes are lost except where the middorsal stripe remains broadest. Gray-brown or dark brown bars or large spots appear laterally overlaying the dorsolateral and ventrolateral dark fields. In some large adult males the lateral light stripes are lost entirely, and the venter becomes blue-white or coppery from chin to vent and onto the ventral surface of the tail.

Females: Juvenile females are similar to juvenile males. Through ontogeny (Fig. 8) the middorsal stripe often becomes interrupted by narrow, dark brown cross-bars. The adult pattern of females is similar to that of adult males, faint to relatively distinct bars appearing in the dorsolateral and ventrolateral dark fields. However, some females lack lateral bars, and the lateral light stripes are retained throughout life.

Color and Pattern in Life.—The dorsal coloration in life of *Ameiva leptophrys* does not differ markedly from that seen in preserved specimens. The middorsal stripe is metallic brown and may have a greenish tint. Paravertebral and lateral light stripes are yellowish to yellowish-gray, and lateral bars or blotches, if present, are yellowish-gray to rust colored. Ventral coloration is variable. The entire ventral surface may be white, cream or copper colored in juvenile males and females. Adults of both sexes may retain these colors, but some adult males become pale blue over the entire ventral surface, or they may have greenish-yellow, orange or brick red on chin, gular region and throat with the ventral surfaces of body, limbs and tail blue. Some adult males exhibit a variation of the latter color pattern in which the hind limbs posterior to the femoral pores and the ventral surface of the tail is copper-colored. Variability in ventral colora-

Fig. 8. Ontogenetic Change and Variation in Pattern of *Ameiva leptophrys*. Males: (A) KU 107555, SVL 85 mm from N slope Cerro Cambutál, Los Santos Prov., Panamá; (B) KU 76142, 115 mm from Barro Colorado Island, Canal Zone, Panamá; (C) KU 95582, 118 mm from 6 km W Palmar Norte, Puntarenas Prov., Costa Rica (included for comparison with KU 76142). Females: (D) KU 95578, 44 mm from 6 km W Palmar Norte, Puntarenas Prov., Costa Rica; (E) KU 76144, 89 mm from Barro Colorado Island, Canal Zone, Panamá; (F) KU 76163, 112 mm from El Valle, Coclé Prov., Panamá. Small males are similar to small females as exemplified by KU 95578 (D above).


A
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tion might be correlated with reproductive condition in these lizards, but this aspect of their biology has not been investigated. It would be instructive to retain specimens in captivity in order to ascertain not only when color changes occur, but whether or not greenish-yellow and orange pigmentation represent stages leading to brick red coloration.

Geographic Variation.—Any analysis of geographic variation of characters of *Ameiva leptophrys* must be considered preliminary, pending the acquisition of additional large samples of specimens from throughout the range of the species. Only four such samples have been available for this study (Fig. 5). There is a noticeable lack of specimens from western Panamá, and the following results should be viewed with both the paucity of large series of specimens and the lack of good geographic representation in mind.

The following characters exhibit no significant geographic differences among sample means (ranges of sample means in parentheses): Supralabials (males, 12.1-12.9; females, 12.4-13.2), infralabials (10.0-10.3), SO-SC values (5.2-6.3) and terminal preanal scales of males (1.9-2.3).

Samples 1 and 2 (Costa Rica) are significantly different from samples 3 and 4 (Panamá) with respect to the following characters (locality number followed by sample mean in parentheses): Number of subdigital lamellae (Sample 1, 29.2; 2, 29.4; 3, 26.5; 4, 27.2), paravertebral granules (1, 45.9; 2, 48.9; 3, 38.1; 4, 37.4) and PV/GAB (1, 0.28; 2, 0.30; 3, 0.25; 4, 0.25). Samples 1, 2 and 3 differ significantly from sample 4, but not from each other, in mean COF values (1, 7.4; 2, 7.3; 3, 8.0; 4, 8.7). One character, total number of femoral pores, shows a significant difference between samples 1 and 2 (1, 43.6; 2, 48.4). In addition to COF values, mentioned above, sample 3 differs significantly from sample 4 in GAB/COR (3, 0.68; 4, 0.65), but sample 4 is not significantly different from samples 1 and 2 (both 0.66). There are a number of characters for which mean values of either sample 1 or 2 differ significantly from that of sample 3, but not from sample 4, and a few (COP, GAB, Longitudinal Rows of Ventrals) for which mean values of sample 1 and/or sample 2 are not significantly different from sample 3, but do differ from the mean value for sample 4.

East-west clines are apparent for a number of characters. In terms of mean values, there is a decrease from east to west (infralabials, longitudinal rows of ventrals) or an increase from east to west (COF values, terminal preanals of females, total preanals of females). If samples 1 and 2 are combined (it is legitimate to do so according to STP results), additional characters show the same clinal tendencies. An increase in mean value from east to west is noted for number of supralabials of males, number of supraoculars, GAB, PV and PV/GAB; decreasing mean values from east to west are noted for COP values. A small sample ($n = 10$) of *leptophrys* from near the Río Sasardí in San Blas Prov., Panamá, was collected by C. W. Myers and arrived too late to be included in the STP analysis. Mean values calculated for each character for the Río Sasardí sample are in accord with the east-west trends discussed above for (Río Sasardí means in parentheses): COF values (2.8), total preanal scales of females (8.4), number of supralabials of males (12.2) and COP values (9.1). The Río Sasardí sample runs counter to east-west trends established on the basis of mean values of samples 1-4 for number of terminal preanals of females (2.0), number of infralabials (10.0), longitudinal rows of ventrals (28.7), number of supraoculars (6.3), GAB (160.1) and PV/GAB (0.24). These results once again call attention to the necessity of obtaining additional samples from intermediate localities before attempting a really

definitive analysis of geographic variation of *leptophrys*.

With the possible exception of color pattern, none of the characters not analyzed by STP appears to vary geographically. Male *leptophrys* from central and eastern Panamá tend to have more emphasis on spotting (rather than bars) in the lateral dark fields then do specimens from western Panamá and Costa Rica. With the acquisition of more specimens from the hiatus in west and central Panamá this difference may also prove to be clinal. In addition, specimens from the Osa Peninsula of Costa Rica (sample 1) appear darker in overall coloration than those collected at other localities, including those from the adjacent non-peninsular mainland of Costa Rica. Since my sample from the Osa Peninsula was collected over a short period of time and by the same collectors, it may be that the darkness of the specimens can be attributed to preservation in warm formalin or to an unusually long period of time in formalin before transfer to ethyl alcohol.

Ecological Notes.—*Ameiva leptophrys* is a forest species; at various localities throughout its range it is found sympatrically with all other species of Middle American *Ameiva*, except *chaitzami*. Hillman (1969) studied niche specificity of *leptophrys*, *festiva* and *quadrilineata* near Rincón on the Osa Peninsula of Costa Rica. He found that adult *leptophrys* forage deeper into the forest than its sympatric congeners; the latter search for food in more open areas. Both *leptophrys* and *festiva* seem to utilize the same areas for basking, but there is little overlap with the more heliophilous *quadrilineata*. Hillman found hatchling *leptophrys* occupying more open areas than the adults but virtually identical to areas utilized by adult *festiva*. Presumably the size difference between juvenile *leptophrys* and adult *festiva* acts to lessen direct competition. In the vicinity of Palmar Norte, Puntarenas Prov., Costa Rica, *festiva* is not abundant, and I found *leptophrys* and *quadrilineata* more closely associated ecologically than either is to *festiva*. The two species were seen basking within a few meters of one another, but whereas *quadrilineata* utilized clearings, *leptophrys* basked in the sun-flecked areas beneath the dense, low vegetation. *Ameiva leptophrys* would allow approach to within a meter before bolting when so hidden. Tree-fall clearings in a swamp forest near Palmar Norte were occupied by juvenile *quadrilineata* and *leptophrys*, but I never found the young of both species utilizing the same clearing. Dunn (1940a) found *leptophrys* and *festiva* sympatric on Barro Colorado Island but reported that *festiva* occupied the more shaded parts of the habitat, whereas *leptophrys* utilized more open areas, the opposite of the situation in Costa Rica. Charles W. Myers (personal communication) found *leptophrys* and *ameiva* sympatric at Guánico Arriba, Los Santos Prov., Panamá. There *leptophrys* occupies dry, partly disturbed forest and *ameiva* is common in open pastures. Recently collected material from near Parrita, Puntarenas Prov., Costa Rica, confirms the sympatry of *leptophrys* and *undulata* hesitantly reported by Dunn (in Stuart, 1942).

Remarks.—Barbour and Loveridge (1929b:213) listed two paratypes of *Ameiva ruthveni* (=*A. leptophrys*): MCZ 10925-10926. Barbour and Noble (1915:471-472) acknowledged examination of only two specimens in their description of *A. ruthveni*: MCZ 9931 (recatalogued MCZ 10927; E. E. Williams, *in. litt.*), the holotype, and MCZ 9932 (recatalogued MCZ 10926). The third lizard, MCZ 10925 (originally MCZ 9928), is not a paratype. One paratype (MCZ 10926) was not located.

Brennan and Yunker (1966:235-236, 258) reported *Ameiva undulata* from Panamá as host for the acarinids *Eutrombicula alfreddugesi* (Oudemans)

and *E. goeldi* (Oudemans). Examination of the specimens of *Ameiva* prove them to be *leptophrys*. There are no valid records of *A. undulata* from Panamá.

Ameiva festiva (Lichtenstein and Von Martens)

Cnemidophorus festivus Lichtenstein and Von Martens, Nomenclator Reptilium et Amphibiorum Musei Zoologici Berolinensis, p. 13, 1856 [Lectotype, herein designated: ZMB 881a; Paralectotype, formerly syntype: ZMB 881b. Type Locality: "Veragua" = Veraguas, Panamá].

Ameiva eutropia Cope, Proc. Acad. Nat. Sci. Philadelphia, 14:62, 1862 [Syntypes: ANSP 9071, USNM 4320(3). Type locality: "Region of the Truando, New Grenada" (=Colombia). Collector: Arthur Schott].

Ameiva edwardsi Bocourt, Ann. Sci. Nat. 17 (17):1-2, 1873 [Holotype: MNHN 5480. Type Locality: Izabel and Santa María de Panzós near Río Polochic, Guatemala. Collector: unknown].

Ameiva festivus—Bocourt, Missión Scientifique au Méxique et dans l'Amerique Centrale; Études sur les reptiles, livr. 3, pp. 260-263, pl. 20A, Fig. 10; pl. 20D, Fig. 3; pl. 20, Fig. 2; 1874.

Ameiva festiva—Günther, Biologia Centrali-Americana; Reptilia and Batrachia, p. 24, 1885. Boulenger, Catalogue of the Lizards in the British Museum (Natural History), vol. 2, p. 347, 1885. Barbour and Noble, Bull. Mus. Comp. Zool., 59(6):473-4, 1915. Burt and Burt, Bull. American Mus. Nat. Hist., 61(5):309, 1931. Burt and Burt, Trans. Acad. Sci. St. Louis, 28(1): 53, 1933. Wettstein, Sitzungsb. Akad. Wiss. Wien, math.-naturw. Kl., Abt. I, 143. Bd., 1.u. 2 Heft., p. 30, 1934.

Ameiva festiva festiva—Dunn, Proc. Acad. Nat. Sci. Philadelphia, 92:114, 1940. Taylor, Univ. Kansas Sci. Bull., 38(1):260-264, 1956.

Ameiva festiva edwardsi—Stuart, Occ. Pap. Mus. Zool., Univ. Michigan, No. 471, p. 21, Figs. 6-7, 1943. Smith and Laufe, Univ. Kansas Sci. Bull. 31(2):64-66, 1945. Smith and Taylor, U. S. Nat'l. Mus. Bull., 199:174, 1950. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, No. 122, p. 77, 1963.

Ameiva festiva occidentalis Taylor, Univ. Kansas Sci. Bull., 38(1):260-264, 1956 [Holotype: FMNH 120236. Type Locality: 8.0 km E San Isidro del General, San José Prov., Costa Rica. Collector: Richard C. Taylor].

Distribution.—*Ameiva festiva* is found in the forests of the Caribbean lowlands from Tabasco, México to Depto. Boyacá, Colombia and on the Pacific lowlands from the vicinity of San Isidro del General, San José Prov., Costa Rica, at least to the Condoto-Andagoya area in the Intendencia de Chocó, Colombia. The species also is known from the vicinity of Tilarán, Guanacaste Prov., Costa Rica, just west of the continental divide (Fig. 9).

Diagnosis.—*Ameiva festiva* can be distinguished from other Middle American *Ameiva* by the following combination of characters: Central gular scales much enlarged, irregular in arrangement; gradual reduction in size of scales radiating outward from enlarged, central gular scales; many femoral pores (mean for males, 40.8; females, 40.0); a transverse row of abruptly enlarged mesoptychial scales; eight longitudinal rows of ventral scutes; a distinct, light colored vertebral stripe present in all but large adults. No other species of *Ameiva* from Middle America possesses such a well-defined vertebral stripe, although several South American *Ameiva* do have such a stripe *(edracantha, orcesi, bridgesi,* and *septemlineata).*

Description.—Maximum observed SVL 114.0 mm. for males, 129 mm. for females; supralabials 12-18 (14.2) for males, 12-17 (13.9) for females; infralabials 8-15 (10.8); sublabials 4-9 (4.7) for males, 4-7 (4.5) for females; supraoculars 4-10 (6.5); COF values 2-6 (2.6); COP values 2-14 (9.4); loreals 2; nostril in prenasal-postnasal suture; prefrontals in contact with postnasal (41.1%) or no (54.5%), 4.5 percent in contact on one side but not the other (n = 448); GAB 145-221 (182.5) for males, 143-213 (179.8) for females; VS 5-29 (12.8) for males, 4-27 (11.2) for females; VS/GAB 0.02-0.14 (0.06); GOR 209-324 (261.1) for males, 215-312 (259.5) for females; GAB/GOR 0.57-0.85 (0.70); SAT 16-22 (18.3); total preanal scales 4-10 (6.6) for males,

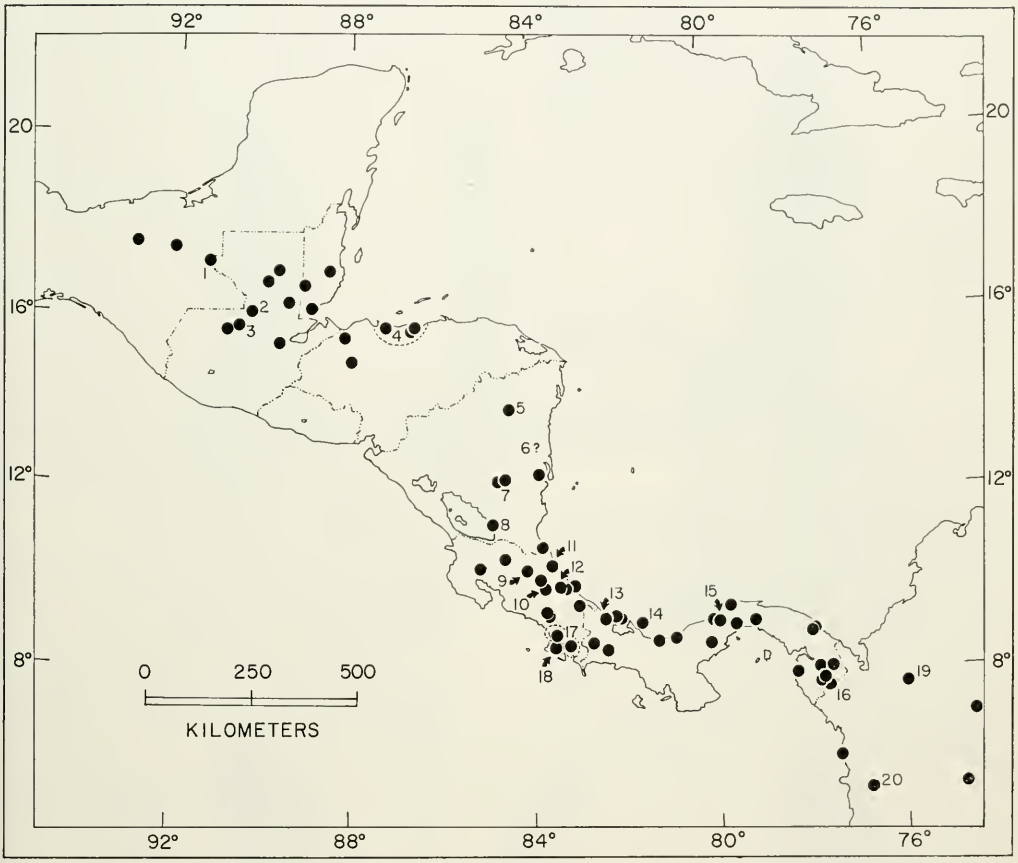


Fig. 9. Map showing locality records of *Ameiva festiva*. To avoid crowding of symbols, some localities have been omitted. Samples used in statistical analyses were (1) Piedras Negras, Depto. El Petén, Guatemala, (2) Vicinity of Chinajá, Depto. Alta Verapaz and Depto. El Petén, Guatemala, (3) Finca Chamá, Depto. Alta Verapaz, Guatemala, (4) North Coast Localities, Honduras, (5) Bonanza, Depto. Zelaya, Nicaragua, (6) Cukra and Kanawa, Depto. Zelaya, Nicaragua, (7) Río Mico and vicinity, Depto. Zelaya, Nicaragua, (8) Tuli Creek, Depto. Río San Juan, Nicaragua, (9) Puerto Viejo, Heredia Prov., Costa Rica, (10) Turrialba, Cartago Prov., Costa Rica, (11) Tortuguero, Limón Prov., Costa Rica, (12) Los Diamantes and vicinity, Limón Prov., Costa Rica, (13) Almirante, Bocas del Toro Prov., Panamá, (14) Isla Escudo de Veraguas, Panamá, (15) Barro Colorado Island, Canal Zone, Panamá, (16) Río Mono, Darién Prov., Panamá, (17) Golfito Region, Puntarenas Prov., Costa Rica, (18) Vicinity of Rincón, Osa Peninsula, Puntarenas Prov., Costa Rica, (19) Río Uré and vicinity, Depto. Córdoba, Colombia, (20) Condoto-Andagoya-Tado Area, Intendencia de Chocó, Colombia.

4-9 (6.4) for females; terminal preanal scales 1-3 (2.0) for males, 1-3 (2.2) for females; one row of enlarged prebrachials; postbrachials enlarged, in a single short row; preantebrachials enlarged, two rows proximally, one distally; three rows of enlarged prefemoral scales; two rows of enlarged tibial scales; femoral pores 33-55 (40.8) for males, 32-50 (40.0) for females; subdigital lamellae 23-34 (28.4); longitudinal rows of ventral scutes 25-33 (27.8); transverse rows of ventral scutes 6-8 (8.0).

Individual variation in posterior head scutellation is great, second only to that of *Ameiva leptophrys*, but two frontoparietal and three parietal scales are usually recognizable (Fig. 10).

Color and Pattern in Alcohol.—

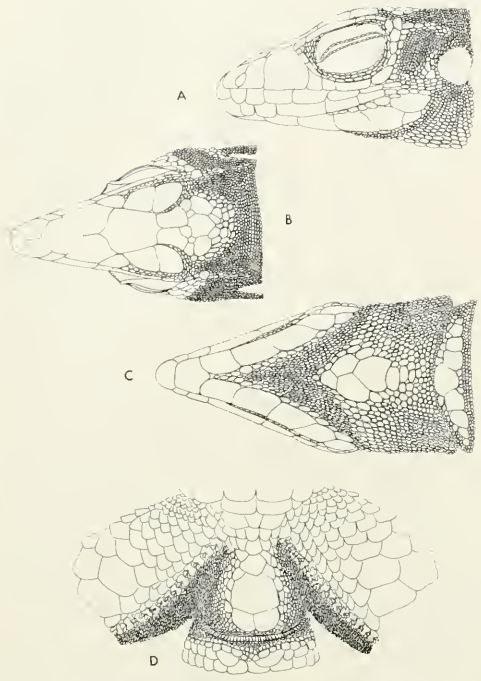


FIG. 10. Head and preanal scutellation of *Ameiva festiva* (ZMB 881a; Lectotype): (A) Lateral view of head, (B) Dorsal view of head, (C) Ventral view of head. × 1.5. (D) Preanal region. × 1.6.

There is extensive geographic variation in color and pattern over the range of *Ameiva festiva*. As a basis for discussing this variation, the following complete description of color and pattern of specimens from Puerto Viejo, Heredia Prov., Costa Rica, is presented.

Juvenile males: Blue-gray vertebral stripe 5-13 granules wide at midbody extending from rostral scale well onto tail, the margins slightly scalloped on the posterior three-fourths of body; top of head lateral to vertebral stripe dark gray; side of head dark gray above becoming lighter below, anterior to eye; ear encircled by interrupted white line; chin, infralabials, gular region and throat light gray or white; dorsal surface of body very dark brown lateral to vertebral stripe; dorsolateral light stripe white, narrow and interrupted, originating on canthus and extending onto tail; dorsolateral dark stripe velvet black, beginning immediately posterior to eye and extending onto tail, bordered below by white, narrow, interrupted ventrolateral light stripe originating beneath eye, passing over ear to the groin, thence onto anterior surface of femur at juncture of dorsal granular scales and enlarged ventral scales; vertical bars extending ventrally from ventrolateral light stripe immediately anterior and posterior to forelimbs; ventrolateral field dark brown with irregular blue-gray spots or narrow, regularly spaced blue-gray bars, or both. Ventral surfaces of body, limbs and tail gray-white. Dorsal surface of forelimbs and femur dark brown to black; shank dark brown with blue-gray spots above.

Through ontogeny (Fig. 11) the vertebral stripe becomes sinuous and less well defined. It may be lost entirely on the head, posterior part of the body and tail. A light-colored rostral scale is retained, as usually is the vertebral stripe on the anterior third of the body. The head becomes uniformly brown above and the pale markings above and below the eye, on the side of the neck and around the ear are lost. The velvet-black dorsolateral dark stripe is retained. In larger individuals, the mid-dorsal area immediately lateral to the position occupied by the vertebral stripe becomes regularly marked with dark and light brown blotches, the darker occupying positions where the sinuous or scalloped margin of the vertebral stripe curved inwards toward the midline; this gives the back a ladder-like pattern. The dorsal surface of the tail becomes uniformly brown or brown with darker brown blotches which may be paired or nearly so. The dorsolateral and ventrolateral light stripes are retained posteriorly only. Most males become blue-gray overall ventrally, the lateral ventral scutes and enlarged femoral scales marked with black. The infralabials may also be flecked with black.

Females: The color and pattern of

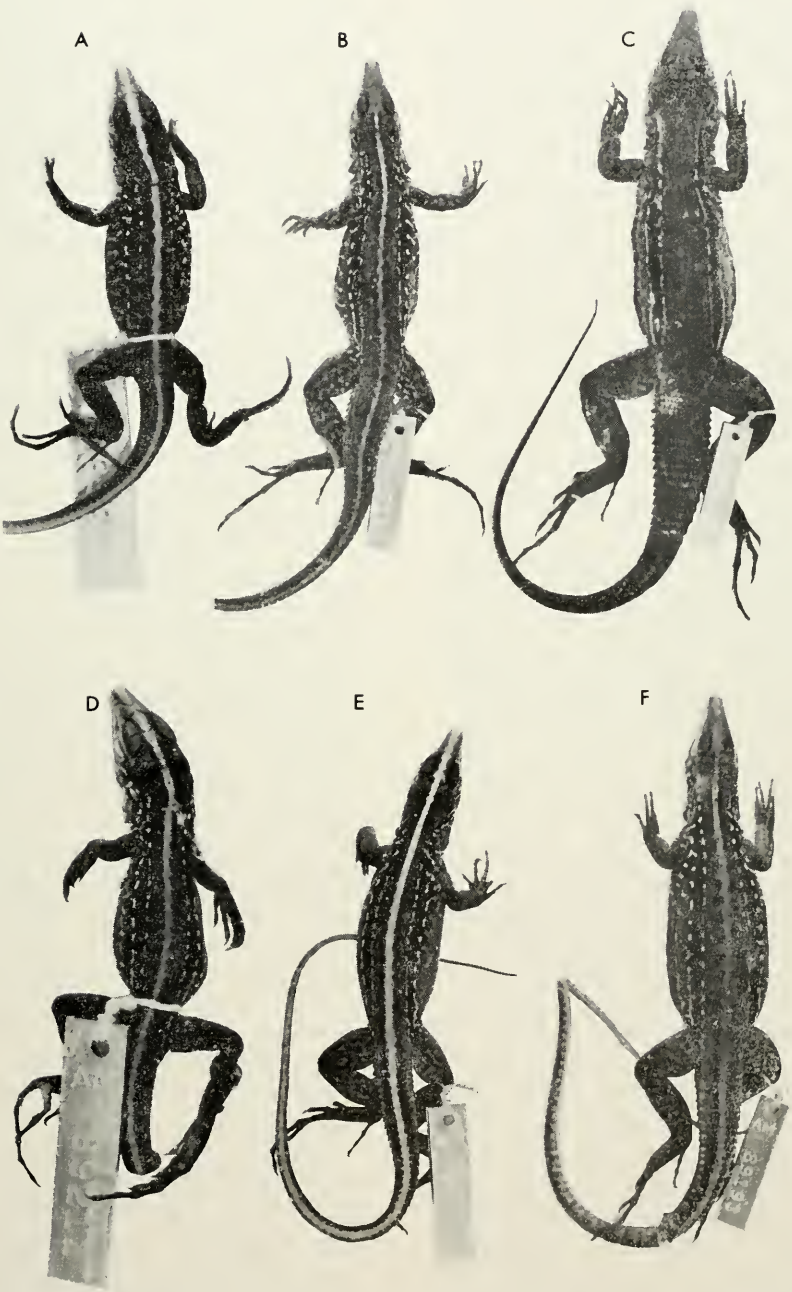


Fig. 11. Ontogenetic Pattern Change of *Ameiva festiva* from the Atlantic Slopes of Costa Rica. Males: (A) AMNH 89210, SVL 43 mm; (B) AMNH 89191, 80 mm; (C) AMNH 89203, 106 mm. Females: (D) AMNH 89212, 47 mm; (E) AMNH 89204, 69 mm; (F) AMNH 89193, 90 mm.

juvenile females is similar to that of juvenile males. Females differ from males in that the juvenile color and pattern is retained with little fading in all but very large adults and adult females do not develop blue colors ventrally.

Color and Pattern in Life.—The following notes refer to specimens collected by me on 1 August 1965 at Puerto Viejo, Heredia Prov., Costa Rica. Adult male (KU 95558), SVL 99 mm: Neck and chest reddish-orange; chin and gular region pale blue; belly pale blue medially and pale blue broken by black blotches laterally; middorsal area brown with indications of a faint yellow vertebral stripe extending from occiput to base of tail; dorsolateral dark field black, bordered above and below by narrow, interrupted yellow stripes; ventrolateral field olive with narrow yellow bars. Adult female (KU 95559), SVL 79 mm: Venter pale bronze; dorsal pattern similar to KU 95558 except vertebral stripe more pronounced and extending from rostral well onto tail; yellow on head and body becoming pale blue on tail.

Juvenile *Ameiva festiva* from near Bluefields, Depto. Zelaya, Nicaragua (KU 101214-101215) possess vertebral stripes which are yellow anteriorly becoming blue-green on the tail. The dorsolateral and ventrolateral light stripes are yellow to yellowish-orange. An adult female (KU 101213) from the same locality has the same color and pattern as KU 95559 from Puerto Viejo.

As in other species of *Ameiva* I have examined, gular coloration varies in adult males. Collections are not such that this can be correlated with season. I suspect the color to be indicative of reproductive state, at least in males, but lack evidence to substantiate this hypothesis. Field notes taken by W. E. Duellman, C. W. Myers, and myself, as well as color photographs provided by D. H. Janzen disclose that the gular region and chest of adult male *festiva* may be uniformly blue (if so, the entire venter is blue), copper, dull brick-red, yellow-orange, golden-yellow or yellow-green (all commonly associated with a blue venter, although individuals having a copper gular region often have the entire venter that color). There seems to be no geographic pattern associated with these colors or none that I can detect from the field notes available to me. The ventral surfaces of females may be uniformly copper or cream (often with a pinkish tint), or may be one of these colors with the gular region and chest gray.

Geographic Variation.—Only the number of transverse rows of ventral scutes and the number of terminal preanals of males show no significant differences among sample means. A number of characters exhibit variation among samples, but show no marked geographic trends. These characters are: GOR, GAB, number of femoral pores, number of longitudinal rows of ventrals, total number of preanal scales and SAT (although SAT values from samples in the Atlantic lowlands may tend to be higher than values from Pacific samples).

A striking aspect of geographic variation among samples of *festiva* is the apparent "center" of variation for certain characters in the Caribbean lowlands of Costa Rica and Nicaragua. Values for VS, VS/GAB, and number of sublabials of males gradually increase in samples to the north and east of these lowlands. A decrease in number of supralabials and in COF values is apparent in the same directions.

A clinal increase in mean values from north (Guatemala) to southeast (Panamá and Colombia) is expressed for GAB/GOR, but samples 17 (Golfito Region of Costa Rica) and 18 (Osa Peninsula of Costa Rica) have high means, nearer to values noted for Samples 16 (Río Mono, Darién Prov., Panamá) and 20 (Condoto-Andagoya-Tado Area, Intendencia de Chocó, Colombia) to the south and east. The mean value

for sample 19 (Río Uré and vicinity, Depto. Córdoba, Colombia) is lower than would be predicted by the trend. A clinal decrease from north to southeast is expressed in number of infralabials (Samples 1 and 19 have lower and higher mean values, respectively, than anticipated by the trend), number of sublabials of females (although high values are noted for samples 14 and 20), COP values (locality 20 has a very low mean and represents a separate subset) and the number of subdigital lamellae. As is evident, these clinal tendencies are never perfectly expressed: one or more samples disrupt the trend. Samples 19 and 20 (in South America) counter in some respects geographic trends established in the more northerly parts of the range of *festiva*. These two localities are separated by high mountains and differ from one another in a statistically significant way for a number of characters. Samples 15 (Barro Colorado Island) and 16 (Río Mono, Darién Prov., Panamá) both show greater similarities to Sample 20 than to Sample 19. Samples 17 and 18, in southeastern Costa Rica, show similarities to Sample 19 for some characters, to sample 20 for others. It would be instructive to have additional samples from the Pacific slopes of western Panamá in order to see whether there is further evidence for the "Panamanian crossover" suggested by Dunn (1940b).

The more northerly samples of *festiva* (Samples 1-4) differ from others in a number of characters, none of which set these samples apart statistically from all others. The samples from Guatemala (Samples 1-3) and Honduras (Sample 4), taken as a group, differ from adjacent samples in a statistically significant way for number of supralabials of males and females, VS of males (data from Sample 4 unavailable) and total preanal scales of females.

As alluded to earlier, there is marked geographic variation in the color and pattern over the range of *festiva*. There are four distinct pattern types with variation to a lesser degree within two of these. The four patterns are discussed separately below relative to the description of specimens from Puerto Viejo, Costa Rica, given above.

Pattern Type A: The color and pattern described for *festiva* from Puerto Viejo is characteristic in major aspects of specimens collected in the Caribbean lowlands of Costa Rica, western Panamá, and northward into México. Lizards comprising Samples 1-7 and possibly 8 (Nicaragua northward) tend to be browner in overall coloration than those from Costa Rica and Panamá (Samples 9-13), although this is a subjective observation and not based upon quantitative evidence. The first impression one gets upon seeing living *festiva* from Costa Rica and Panamá is one of a black lizard with a prominent vertebral stripe. The lizards from Honduras and Guatemala have a broader vertebral stripe than others with Pattern Type A; this is especially striking in specimens from Guatemala.

Pattern Type B: A second widely distributed pattern type, largely allopatric to Pattern Type A, is peculiar to lizards from the Pacific slopes of southeastern Costa Rica and western Panamá, the San Blas Coast of Panamá and Colombia east of the Cordillera Central (Samples 15-19). Specimens from this area are characterized by a relatively broader vertebral stripe than that of other pattern types and by having the ventrolateral light stripe either lacking, present or present only posteriorly. The vertebral stripe broadens posteriorly and is broadest in specimens from eastern Panamá and Colombia. Lizards from the San Blas Coast of Panamá and from east of the Cordillera Central in Colombia possess vertebral stripes that may become as broad as the middorsal area at the base of the tail (Fig. 12B). *Ameiva festiva* from the Osa Peninsula of Costa Rica (Sample 18) are darker in overall coloration than those from the

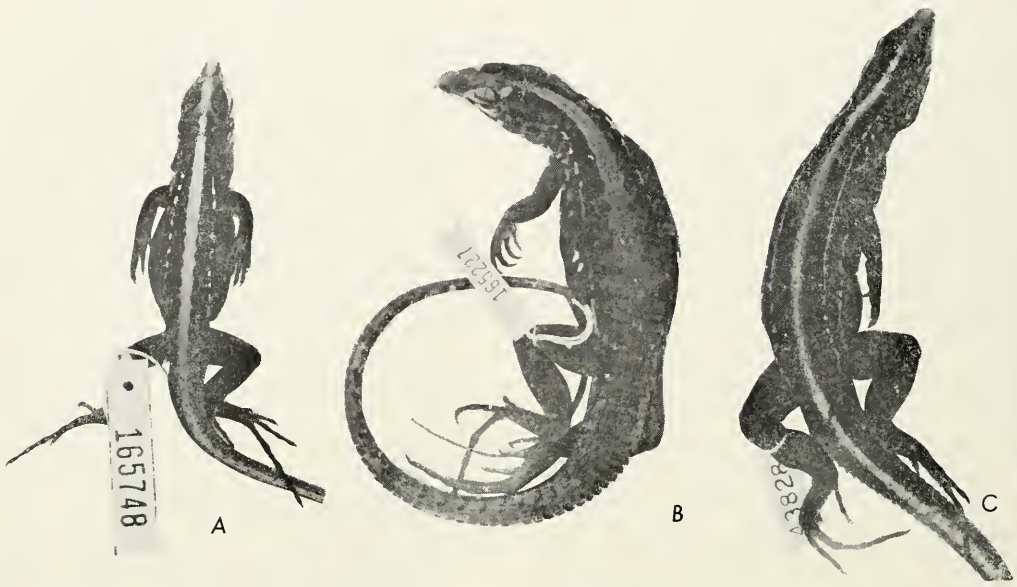


FIG. 12. Patterns of *Ameiva festiva* from Colombia. (A) FMNH 165748, male, SVL 44 mm, from the Upper Río Uré, Depto. Córdoba. (B) FMNH 165227, male, 101 mm, from the Upper Río Uré, Depto. Córdoba. (C) FMNH 43828, female, 81 mm, from Pizzaro, Intendencia de Chocó (?).

adjacent mainland. This is not the result of preservation, for color photographs taken by Daniel H. Janzen before the lizards were preserved show them to be darkly pigmented. Two specimens of *festiva* (KU 80210 and KU 110745) from Almirante, Bocas del Toro Prov., Panamá, exhibit a pattern similar to that described here, although others from the same locality show Pattern Type A. *Ameiva festiva* from Barro Colorado Island and southeastern Panamá are somewhat intermediate between Pattern Types A and B, but because the population more closely resembles the latter, I have included them here.

Pattern Type C: *Ameiva festiva* from the Chocó of Colombia (including Sample 20) have a pattern similar to Type A, but the vertebral stripe is extremely straight and well defined even in large specimens (Fig. 12C). The dorsolateral and ventrolateral light stripes are also well defined, may be entire or dotted (rarely dashed), and are not lost in large individuals. Preserved specimens are, with the exceptions of the light stripes and vertebral stripe, very dark.

Pattern Type D: Adult *Ameiva festiva* from Isla Escudo de Veraguas, off the northwest coast of Panamá, are melanistic. That this is so is supported by color photographs of freshly collected specimens provided by Charles W. Myers. Very little pattern is apparent on specimens I have examined and, although examination of juvenile specimens (unavailable to me) might prove them to belong to Pattern Type A or B, I prefer to assign them to a separate pattern type for the present. Baskin and Williams (1966) summarized information on insular populations of melanistic *Ameiva* in the Caribbean, and Mayr (1963) discussed similar populations of *Lacerta* in the Mediterranean. Such melanistic island populations are usually found on small, dry, barren islands (Mayr, 1963); Heatwole and Torres (1966) attributed the phenomenon in *Ameiva* to local differentiation, those species of *Ameiva* exhibiting melanism not being closely related.

Mayr (1963) suggested that the dark pigmentation might function in heat regulation. The sample from Isla Escudo de Veraguas does not fit the pattern in terms of habitat as outlined above. According to C. W. Myers (personal communication), one of the few biologists to have visited the island, Isla Escudo de Veraguas ". . . is covered with humid forest, including swamp forest, except for a well developed line of strand vegetation at some points." Specimens of *festiva* from the Bocas del Toro Archipelago to the west of Isla Escudo de Veraguas are not notably melanistic and conform to Pattern Type A, although, according to Myers, habitats on all of these islands are similar. That the melanism of *festiva* on Isla Escudo de Veraguas is the result of local differentiation can hardly be denied, but the adaptive significance of such pigmentation remains a mystery.

Ecological Notes.—In the northern part of its range, *Ameiva festiva* inhabits heavy forest (Stuart, 1943; Smith and Laufe, 1946; Echternacht, 1968) when sympatric with other macroteiids. If other large teiids are not present, the niche of the species is expanded to include more open habitats (Echternacht, 1968). In México, Guatemala, and Honduras, *festiva* is partly sympatric with *undulata* and with various species of *Cnemidophorus*. In Costa Rica and Panamá, *festiva* and either *leptophrys* or *quadrilineata,* or all three species may occur together. In the vicinity of Almirante and on the islands of the Bocas del Toro Archipelago, Bocas del Toro Prov., Panamá, *festiva* and *quadrilineata* are sympatric, as they are on Isla Escudo de Veraguas. *Ameiva festiva* typically occupies the more shaded parts of the habitat, whereas *quadrilineata* occurs in the open (C. W. Myers, personal communication). In southeastern Costa Rica (vicinity of San Isidro del General, San José Prov.; vicinity of Palmar Sur and on the Oso Peninsula, Puntarenas Prov.) *festiva* is sympatric with both *quadrilineata* and *leptophrys*. *Ameiva festiva* occupies a habitat intermediate to those of the other two species: *leptophrys* occupies more shaded areas and *quadrilineata,* the open areas. This has been noted by Hillman (1969) and myself, but Dunn (1940a) reported the habitats of *leptophrys* and *festiva* reversed on Barro Colorado Island in Panamá; there *festiva* occupies the less shaded areas. Hillman (1969) found hatchling *A. leptophrys* sympatric with adult *festiva* on the Osa Peninsula and concluded that the difference in size between the two minimizes competition. The reproductive biology of *festiva* has been investigated by R. E. Smith (1968a, b) in the only such study of *Ameiva* that has been undertaken. Smith's results suggest that *festiva* is reproductively active throughout the year, and that clutch sizes average between 2.22 and 2.29 eggs.

Nothing has been reported on the ecology of *A. festiva* in South America.

Remarks.—*Ameiva festiva* was described by Lichtenstein and von Martens (1856) on the basis of two specimens, which are catalogued under one number (ZMB 881) in the Zoological Museum of Berlin. The description is based on a specimen "Long. a rostro ad caud. bas. 3 1/2″, caud. ultra 6″″ (88.9 mm). The syntypes presently have snout-vent lengths of 86 and 58 mm; the tail of the larger is broken. I am herein designating the larger syntype as the lectotype; shrinkage resulting from over one hundred years in preservative would account for the discrepancy in snout-vent length between that given in the description and my measurement. The smaller syntype becomes a paralectotype.

Dunn (1943) described *Ameiva festiva nicefori* from Saisima, Depto. Cundinamarca, Colombia, but I have presented evidence elsewhere (Echternacht, 1970) that the population deserves specific recognition. Dunn (1940a) and Villa (1968) allied the population

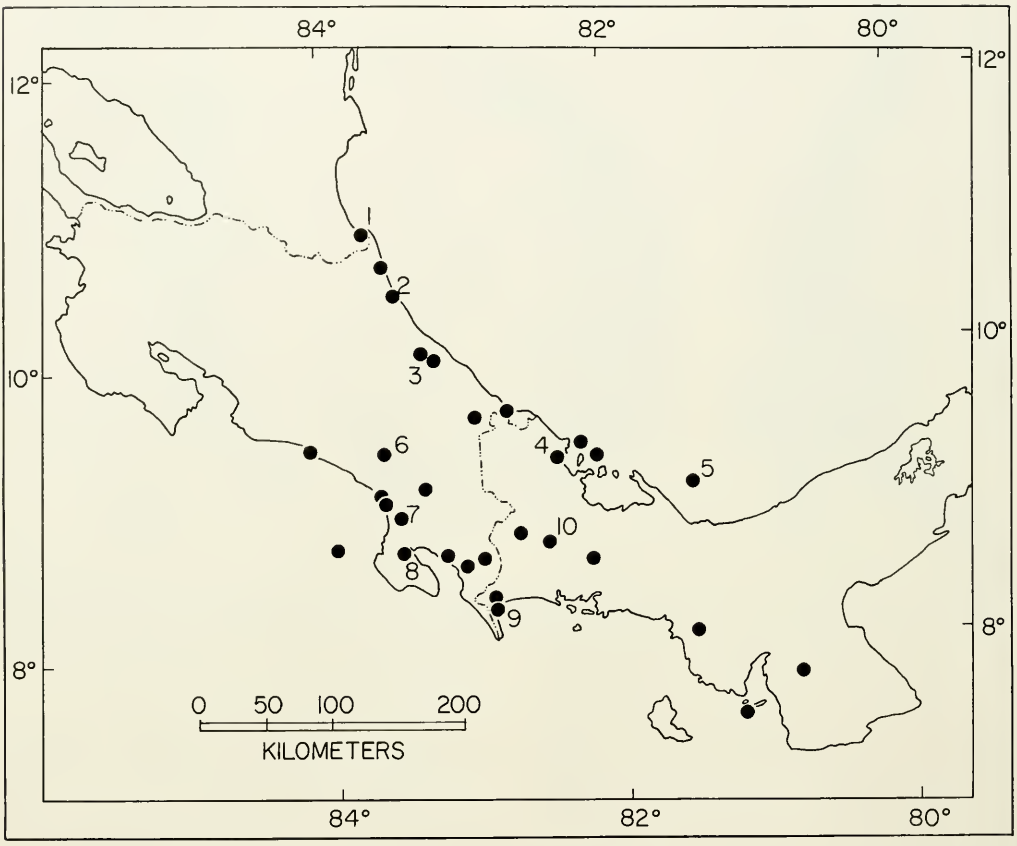


Fig. 13. Map showing locality records of *Ameiva quadrilineata*. To avoid crowding of symbols, some localities have been omitted. Samples used in statistical analyses were (1) Southeastern Nicaragua, (2) Tortuguero, Limón Prov., Costa Rica, (3) Limón and vicinity, Limón Prov., Costa Rica, (4) Bocas del Toro Prov., Panamá, (5) Isla Escudo de Veraguas, Panamá, (6) San Isidro del General, San José Prov., Costa Rica, (7) Palmar Sur and vicinity, Puntarenas Prov., Costa Rica, (8) Vicinity of Rincón, Osa Peninsula, Puntarenas Prov., Costa Rica, (9) Progreso, Puerto Armuelles and vicinity, Chiriquí Prov., Panamá, (10) Boquete, Chiriquí Prov., Panamá.

of *Ameiva* on the Islas del Maiz, Nicaragua with *undulata* rather than *festiva* as originally described (Barbour and Loveridge, 1929a). My investigations support this conclusion, and the population is discussed with *undulata* in the present work.

Ameiva quadrilineata (Hallowell)

Cnemidophorus quadrilineatus Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1860, p. 483, 1860 [Syntypes: USNM 6053A, 6053B. Type Locality: "Nicaragua," restricted to Greytown, Depto. Río San Juan, by Taylor, Univ. Kansas Sci. Bull., 38(1):271, 1956].

Ameiva quadrilineata—Cope, Proc. Acad. Nat. Sci. Philadelphia, 1862, p. 61, 1862. Bocourt, Mission Scientifique au Méxique et dans l'Amerique Centrale, Études sur les Reptiles, livr. 4, p. 259, pl. 20A, Fig. 9, 1874. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 24, 1885. Dunn, Proc. Acad. Nat. Sci. Philadelphia, 92:113, 1940. Taylor, Univ. Kansas Sci. Bull., 38(1):271, 1956.

Ameiva gabbiana Cope, J. Acad. Nat. Sci. Philadelphia, ser. 2, 8:33, pl. 28, Fig. 3, 1875 [Syntypes: USNM 32614-16. Type Locality: Old Harbor (= Puerto Viejo), Limón Prov., Costa Rica. Collector: W. M. Gabb]. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 23, 1885.

Ameiva undulata—Boulenger, Catalogue of the Lizards in the British Museum (Na-

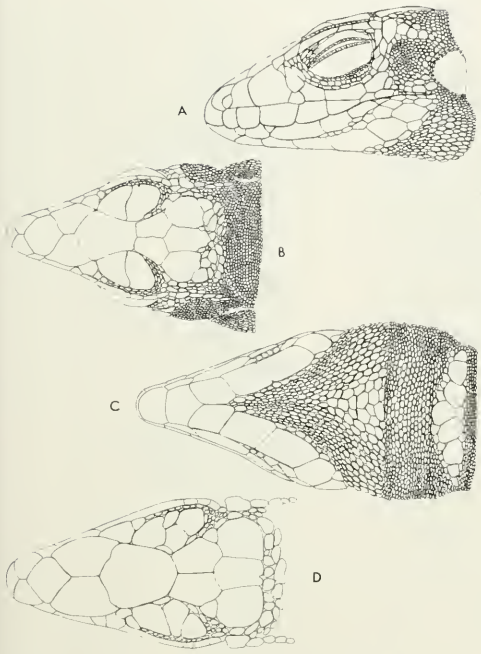


Fig. 14. Head scutellation of *Ameiva quadrilineata*: (A) Lateral view of head, (B) Dorsal view of head, (C) Ventral view of head; KU 95593 from 1.5 km E Palmar Norte, Puntarenas Prov., Costa Rica, × 2. (D) Dorsal view of head; KU 96849 from Cayo Zapatillo Grande, Bocas del Toro Prov., Panamá, × 2.7.

tural History), 2nd Ed., vol. 2, p. 348, 1885 (part).

Distribution.—Atlantic coastal lowlands from extreme southeastern Nicaragua to northwestern Panamá; Pacific slopes of Costa Rica from Quepos, Puntarenas Prov. (H. S. Fitch, personal communication) to the Azuero Peninsula, Panamá; the Bocas del Toro Archipelago, Isla Escudo de Veraguas and Isla de Cebaco of Panamá and Isla del Caña of Costa Rica. Specimens have been collected at elevations of 1100-1650 m above Paso Ancho and on Cerro Hornito, Chiriquí Prov., Panamá (Fig. 13).

Diagnosis.—A small lizard which can be distinguished from other Middle American *Ameiva* by the following combination of characters: Central gular scales moderately enlarged, irregular,

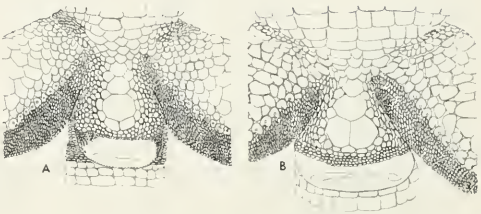
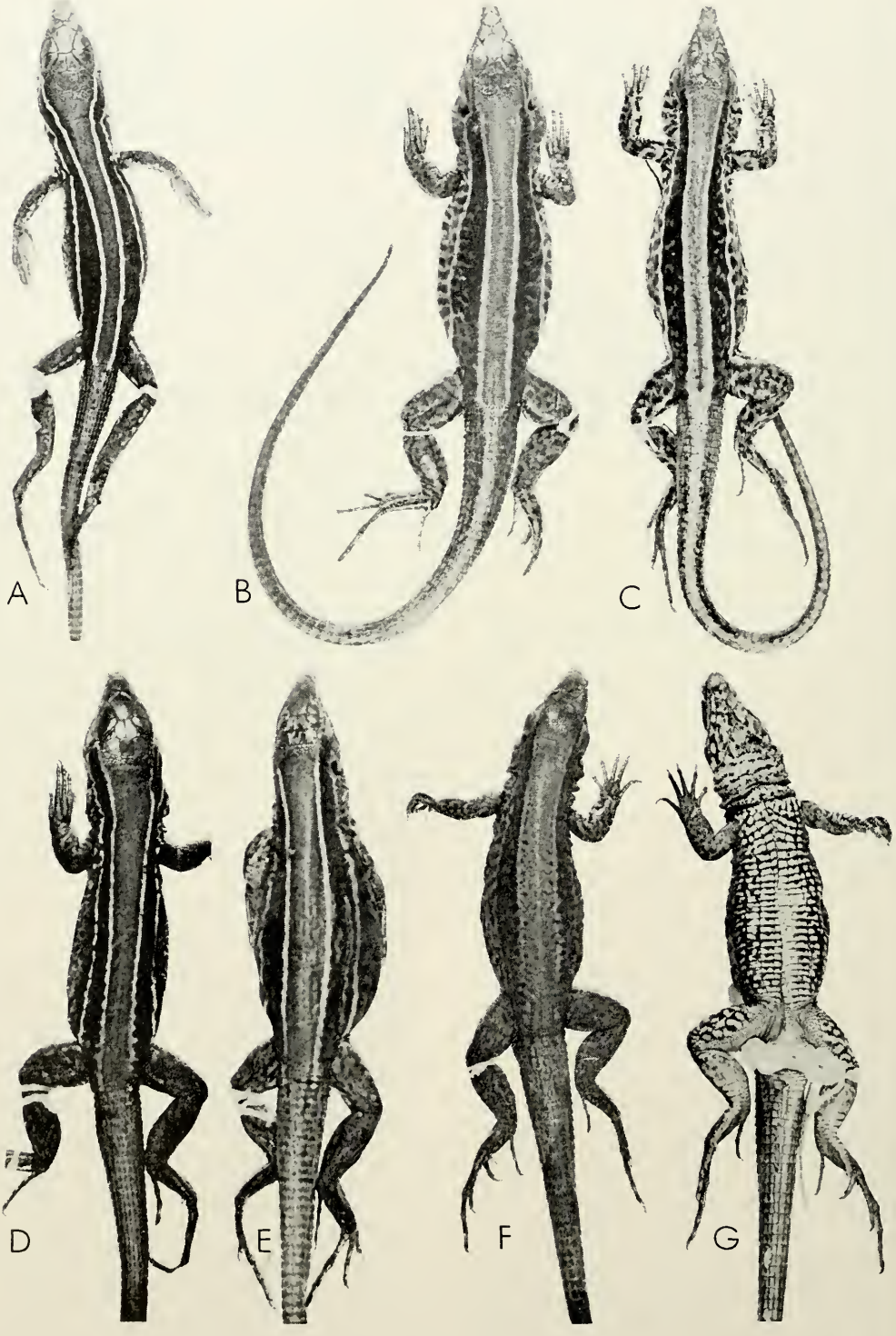


Fig. 15. Preanal region of *Ameiva quadrilineata*: (A) KU 95636 from 6 km W Palmar Norte, Puntarenas Prov., Costa Rica, × 2. (B) KU 95593 from 1.5 km E Palmar Norte, Puntarenas Prov., Costa Rica, × 2.

scales of posterior one-half of gular region abruptly smaller than scales of anterior one-half (Figs. 14-15); moderate number of femoral pores (mean number for males, 34.2; females, 27.8); a transverse row of abruptly enlarged mesoptychial scales; eight longitudinal rows of ventral scutes; narrow middorsal field (mean PV: 26.1) which does not become darker laterally; continuous, well defined dorsolateral stripe and continuous to interrupted ventrolateral stripe, both usually retained throughout life. The middorsal field of *Ameiva undulata* is broad (mean PV: males, 46.8; females, 45.6) and the ventrolateral light stripe is usually interrupted. *Ameiva chaitzami* also has a relatively broad middorsal field (mean PV: 38.1) and interrupted ventrolateral light stripes and, in addition, lacks a uniformly colored middorsal field.

Description.—Maximum observed SVL 88 mm for males, 82 mm for females; supralabials 11-16 (13.7); infralabials 10-13 (10.1); supraoculars 6-9 (6.7); COF values 2-6 (3.0); COP values 4-12 (9.1); loreals 2-4; nostril in prenasal-postnasal suture; prefrontals in contact with postnasals; GAB 116-177 (140.5); PV 16-36 (26.1); PV/GAB 0.09-0.25 (0.19); GOR 185-258 (218.6); GAB/GOR 0.41-0.78 (0.64) for males, 0.56-0.75 (0.64) for females; SAT 17-22 (19.8) for males, 17-21 (19.5) for females; total preanal scales 4-10 (7.1) for males, 4-9 (6.8) for females; terminal preanal scales 1-3 (1.4) for males,


A
B
C
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1-3 (1.3) for females; prebrachials enlarged, in a single row; postbrachials moderately enlarged, in one row or irregular; preantebrachials in three rows proximally, one or two rows distally; three rows of enlarged prefemoral scales; infratibials enlarged, in two rows; femoral pores 22-42 (34.2) for males, 18-39 (27.8) for females; subdigital lamellae 25-34 (29.5) for males, 25-34 (28.8) for females; longitudinal rows of ventral scutes 28-33 (29.8); transverse rows of ventral scutes 4-10 (8.0).

Color and Pattern in Alcohol.—Juvenile males: Top of head light brown to gray-brown; side of head gray with black wash above grading to gray on lower half of postnasals, loreals and supralabials; middorsal field dark brown to dark gray-brown, narrow, bounded laterally by narrow, white dorsolateral light stripes, which originate above the eyes and extend to the base of the tail where they coalesce and form a vertebral stripe extending well onto the tail; dorsolateral dark fields black; ventrolateral light stripe narrow, white, originating beneath eye and extending to the groin, thence onto anterior surface of femur where it runs between the dorsal granular scales and the ventral plates; short, narrow, interrupted white stripe from beneath ear to shoulder; ventrolateral dark field black with brown mottling below; dorsal surfaces of forelimbs mottled brown and black, an interrupted white line extending along the back of the arm from shoulder to wrist; dorsal surface of hind limbs mottled black and brown with white spots on shank and narrow, white postfemoral stripe extending onto tail for ca. 10-12 scale whorls; ventral surfaces immaculate except for faint gray markings in the gular region and a faint, transverse gray line across the gular region at the juncture of the large anterior and small posterior scales.

Through ontogeny (Fig. 16) black mottling appears in the middorsal area, but never enough to disrupt the visual impression of a unicolored field. Gray or blue-gray reticulations appear in the ventrolateral dark field, this pattern extending onto the lateral-most enlarged ventral scutes and the enlarged ventral femoral scales. The dorsolateral dark field remains black above, but brown vertical bars or reticulations appears in the lower half. The white spots on the hind limbs and the short stripe between ear and shoulder disappear, the side of the neck becoming uniformly gray-brown or black with gray reticulations. Ventral surfaces may be pale blue overall or the chin, gular region and throat may be salmon colored, the remainder of the venter pale blue. There may be black flecks in the midventral region (see discussion of geographic variation).

Females: Juvenile females resemble juvenile males. Adult females tend to retain the juvenile pattern except that black flecking appears in the middorsal field and small, brown, longitudinally oriented flecks and blotches may appear in the dorsolateral dark field (Fig. 16).

There is some geographic variation in color and pattern and the foregoing description applies to specimens from the Pacific lowlands of Costa Rica.

Color and Pattern in Life.—The fol-

Fig. 16. Ontogenetic change and variation in pattern of male *Ameiva quadrilineata*. A-C; Pacific population. D-G; Atlantic population. Females do not show marked ontogenetic changes in color or pattern and resemble juvenile males as to these characters. (A) KU 95623, SVL 31 mm, from the Río Zapote, 8 km E Palmar Norte, Puntarenas Prov., Costa Rica; (B) KU 95583, 68 mm, from 8 km SE San Isidro del General, San José Prov., Costa Rica; (C) KU 93984, 84 mm, from 2-5 km ESE Piedras Blancas, Puntarenas Prov., Costa Rica; (D) KU 96837, 40 mm, from Isla Bastimentos, Bocas del Toro Prov., Panamá; (E) KU 108282, 62 mm, from E end Isla Escudo de Veraguas, Panamá; (F) KU 96845, 79 mm, from Cayo Zapatillo, Bocas del Toro Prov., Panamá; (G) Ventral view of KU 96845 to show dark pigmentation.

lowing description is extracted from the field notes of C. W. Myers and refers to a series of *Ameiva quadrilineata* (KU 96853-96865) collected 13 km N Puerto Armuelles, Chiriquí Prov., Panamá, on 22 April 1965. *Ameiva quadrilineata* from this locality do not differ in color and pattern from individuals found in the Pacific lowlands of Costa Rica, the latter having been used for the description of color and pattern in alcohol. The following account (modified from Myers' field notes) serves to illustrate the variability of ventral pigmentation.

Dorsolateral and lateral stripes vivid yellow in small individuals and somewhat duller in larger ones; dorsolateral stripes nearly disappearing in largest males. Middorsal region light yellow-brown or gray-brown, with or without irregular black spotting, and turning to a whitish-gray or pale brown dorsal stripe on basal one-third of tail. Venter of tail base copper, but all but basal part of tail is uniformly brown or gray above and below (in a juvenile male this tail is light blue-gray). Dorsolateral area of body (between yellow stripes) bright rust, variably suffused with black (in some nearly uniformly black with rust spots). Flanks light brown or light gray-brown, heavily spotted with black. Ventral color variable, as follows: KU 96853-5—3 juveniles (at least two are males): Ventral surfaces pale copper. KU 96856-9—4 females: Ventral surfaces pale copper, perhaps with a yellow tinge on throat. KU 96860-1—2 males: Underside of head pale blue; rest of venter light blue, except tail base and thighs behind femoral pores, which are light copper. KU 96862-3—2 males: Underside of head light coppery orange; rest of venter light blue, except for copper thighs behind femoral pores, and light blue and copper-mottled tail base. KU 96864-5—2 males: Underside of head red-orange (pale in smaller specimen and deep in larger) with an occasional speck or spot of blue showing through; rest of venter light blue, except rear of thighs, and tail base (copper).

In addition to the ventral colors given above, both males and females of all sizes may have immaculate or pearly-white ventral surfaces. The chin, gular region and throat may be various shades of yellow.

Geographic Variation.—The range of *Ameiva quadrilineata* is divided by the high mountains of the Cordillera de Talamanca of Costa Rica and Panamá. Although the resulting Atlantic and Pacific populations do not show statistically significant differences for any characters, it is apparent that divergence has taken place. Mean values for number of femoral pores of females and number of terminal preanals of both sexes are higher and lower, respectively, on the Atlantic slope than on the Pacific. The mean number of terminal preanal scales of females from Boquete, Chiriquí Prov., Panamá (Sample 10), is statistically different from mean values of all other samples and constitutes a separate subset. Several other characters show similar trends, but with one sample running counter to the trend established by the others. Characters having lower values along the Atlantic slope are GAB, GAB/GOR for both sexes, and total number of preanal scales for both sexes. The sample from Boquete, which is intermediate in geographic position to Puerto Armuelles (Pacific slope) and Almirante (Atlantic slope) in Panamá, has intermediate mean values to those of Puerto Armuelles and Almirante for some characters and more closely resembles samples from the Atlantic slope than those from the Pacific slope for other characters. Boquete lies on the Pacific slope of the Cordillera de Talamanca but a few kilometers from the continental divide in western Panamá. Sample 10 has intermediate values for number of supralabials, PV, and SAT of males. Mean values for number of supraoculars, GAB, GAB/GOR of males and females,

and total number of preanals of both sexes are nearer mean values for Atlantic samples than for Pacific samples. Occasionally, other samples on the Pacific slope resemble the aggregate of Atlantic slope samples in terms of mean values of one character or another, but none with such noticeable frequency as does Sample 10.

Samples 8, 9 and 10 show a statistical relationship to one another for several characters and constitute a separate subset for COF and COP values. Samples 8 and 9 on a separate subset for GAB, having very high means for this character. For GAB, Sample 10 has the lowest observed mean value and is similar to Atlantic slope samples in this. Sample 6 has the lowest observed mean PV and constitutes a separate subset.

General clinal tendencies are noted for some characters. The total number of preanal scales decreases from north to south on the Atlantic slopes, but increases from north to south in samples from the Pacific slopes (except Sample 10, which has a very low mean); COP values decrease from north to south on the Pacific side; COF values increase from north to south on the Pacific slope; the number of subdigital lamellae of females decreases from north to south on the Atlantic slope. Inclusion of more samples in the analysis is necessary in order to substantiate these trends.

Mean values for total number of infralabials and for numbers of rows of longitudinal and transverse ventral scutes show no significant differences among the ten samples.

Some geographic variation is apparent in the color and pattern of *Ameiva quadrilineata.* Although specimens from Atlantic and Pacific slope populations do not differ markedly among themselves, there are differences between the two populations. Adult males from the Atlantic side are never as ornate in terms of dorsal and lateral color and pattern as those from the Pacific slopes (Fig. 16). Males from the Atlantic slopes, especially those from northwestern Panamá (including Samples 4 and 5) have all ventral surfaces variably flecked with black (Fig. 16); the dorsolateral light stripes of specimens from this area may be scalloped over the posterior third of the body and may become diffuse, blending with middorsal coloration, in large individuals; the lateral light stripe may be interrupted and the dorsal caudal stripe is less evident; the lateral ground color of some adults is black mottled with brown above, gray below. In general, it seems that the chin, gular region and throat of adult male *quadrilineata* from the Atlantic slopes becomes yellow when brightly pigmented, but that such lizards from the Pacific slopes show red or orange coloration. I know of only one exception to this: KU 95600 collected at Quebrada Boruca at the Río Puente Nuevo, 22 km E Palmar Norte, Puntarenas Prov., Costa Rica, on 15 August, 1965, was yellow on the ventral surface of the head. This generality needs to be substantiated; I have had no color-in-life notes on Atlantic slope specimens from west of the Bocas del Toro region of Panamá.

Ameiva quadrilineata from Isla Escudo de Veraguas of Panamá and from the Osa Peninsula of Costa Rica do not appear to be any darker in coloration than those from the adjacent mainlands.

Ecological Remarks.—Ameiva quadrilineata is ecologically the best known member of the genus (Hirth, 1963, 1965; R. E. Smith, 1968a, b). Both Hirth and Smith worked with populations of *quadrilineata* on the Atlantic lowlands, Costa Rica. Hirth (1963) studied all aspects of the ecology of *A. quadrilineata* at Tortuguero, Limón Prov., Costa Rica. At Tortuguero these lizards were abundant on the beaches, which they shared with *Basiliscus vittatus. Ameiva quadrilineata* is also characteristic of the beach fauna on the islands of the Bocas del Toro Archipelago and Isla Escudo de Veraguas of Panamá (C. W. Myers,

personal communication) and near the northern (western) limit of its range on the Pacific coast of Costa Rica (H. S. Fitch, personal communication). I have collected it in open areas (clearings in forested areas, along roadsides, etc.) near San Isidro del General and Palmar Norte in southeastern Costa Rica. Dunn (1940a) reported the species to be common in open areas along large rivers on the Atlantic side of Costa Rica. Hillman (1969:477), who studied *quadrilineata* on the Osa Peninsula of Costa Rica, found them foraging "in low vegetation adjacent to an exposed surface such as a road." The species is definitely more heliophilic than either *festiva* or *leptophrys*, with which it is sympatric in some areas. It is similar in habitat preference to *ameiva*. The relatively small size of adult *quadrilineata* undoubtedly helps to reduce competition between it and its larger, sympatric congeners. Competition may be relatively more intense between juvenile *quadrilineata* and juvenile *leptophrys* or *festiva*. I have no experience with *festiva* on this point, but I found juveniles of the other two species common in tree-fall clearings in a swamp forest near Palmar Norte in Costa Rica. The clearings were always occupied by one of the two, but not both species.

R. E. Smith (1968a, 1968b) studied *Ameiva quadrilineata* and *festiva* at Pandora, Limón Prov., Costa Rica. His investigations indicate that both species may be reproductively active throughout the year. The mean clutch size for *quadrilineata* is 2.05-2.07 eggs, depending upon method of counting, and oviposition occurs between 17 and 21 days following ovulation. Smith also discussed the adaptive significance of fat bodies and provided experimental evidence for a relationship between fat body development and gonadal cycles.

Ameiva are usually diurnal, but W. E. Duellman (personal communication) found an adult male *quadrilineata* active at night on a road in western Panamá. There had been a heavy rain earlier in the day, and possibly the lizard was flooded from its burrow.

Henry S. Fitch (personal communication) is studying a population of *quadrilineata* near Quepos, Puntarenas Prov., Costa Rica. The nearest locality from which specimens of *undulata* are available is near Parrita, about 25 km to the northwest, but Fitch has observed both species at Quepos. There *quadrilineata* occurs only on the beach, and *undulata* is inland in plantations or pastures where shade and ground cover are abundant. Quepos is the northern-most locality for *quadrilineata* on the Pacific coast, and the southern-most locality for *undulata*.

Remarks.—Barbour and Noble (1915) apparently confused *Ameiva quadrilineata* and *A. undulata pulchra*. Both were described by Hallowell (1860) from "Nicaragua," but *quadrilineata* is restricted to the Atlantic coast of Nicaragua and *pulchra* to the Pacific coast; Barbour and Noble had before them specimens from "Chinandega, Nicaragua," which is on the Pacific side. Moreover, the color description given by Barbour and Noble fits that of *undulata*, not *quadrilineata*.

Ameiva undulata (Wiegmann)

Cnemidophorus undulatus Wiegmann, Herpetologica Mexicana, pp. 27-28, 1834 [Syntypes: ZMB 867-869, 869 missing. Type Locality: "Mexico," restricted to Tehuantepec, Oaxaca, México by Hobart M. Smith, Proc. Biol. Soc. Washington, 53:56, 1940. Collector: Unknown].

Ameiva undulatus—Gray, Catalogue of the lizards in the British Museum (Natural History), p. 20, 1845.

Ameiva undulata—Cope, Proc. Acad. Nat. Sci. Philadelphia, 14:62-63, 1862. Bocourt, Mission Scientifique au Mexique et dans l'Amerique Centrale; Études sur les reptiles, livr. 3, pp. 254-259, pl. 20A, Fig. 7a-7e, pl. 20B, Fig. 1. Günther, Biologia Centrali-Americana; Reptilia and Batrachia, pp. 23-24, 1885. Boulenger, Catalogue of the lizards in the British Museum (Natural History), vol. 2, pp. 347-348, 1885. Hartweg and Oliver, Occas. Papers Mus. Zool., Univ. Michigan, 359:7-8, 1937. Dunn,

Proc. Acad. Nat. Sci. Philadelphia, 92:114-115, 1940.

Ameiva pulchra Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 483, 1860 [Syntypes: ANSP 9133-9134. Type Locality: "Nicaragua." Collector: Unknown].

Cnemidophorus amivoides Cope, Proc. Acad. Nat. Sci. Philadelphia, pp. 198-199, 1894 [Holotype: AMNH 16316. Type Locality: La Carpintera, San José Prov., Costa Rica. Collector: A. Alfaro].

Ameiva undulata undulata—Barbour and Noble, Bull. Mus. Comp. Zool., 59(6):474-475, 1915. Stuart, Proc. Biol. Soc. Washington, 55:145, 1942. Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):62-64, Fig. 2b, 1946. Smith and Taylor, U. S. Natl. Mus. Bull., 199:174, 1950.

Ameiva undulata parva Barbour and Noble, Bull. Mus. Comp. Zool., 59(6):476-477, 1915 [Holotype: MCZ 5831. Type Locality: "Guatemala," restricted to Mazatenango, Depto. Suchitepequez by Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):51, 1946. Collector: Unknown]. Stuart, Proc. Biol. Soc. Washington, 55:145, 1942. Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):51-54, Fig. 1a, Pl. Ia, 1946. Smith and Taylor, U. S. Natl. Mus. Bull., 199: 173, 1950. Taylor, Univ. Kansas Sci. Bull., 38(1):268-271, 1956. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 122:77, 1963.

Ameiva undulata pulchra—Dunn, Proc. Acad. Nat. Sci. Philadelphia, 92:115, 1940. Stuart, Proc. Biol. Soc. Washington, 55: 146, 1942.

Ameiva undulata hartwegi Smith, Proc. Biol. Soc. Washington, 53:55, 1940 [Holotype: USNM 108600. Type Locality: Across the Río Usumacinta from Piedras Negras, Depto. El Petén, Guatemala. Collector: H. M. Smith]. Stuart, Proc. Biol. Soc. Washington, 55:145, 1942. Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):35-36, Pl. IIb, 1946. Smith and Taylor, U. S. Natl. Mus. Bull., 199:171-172, 1950. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 122:77, 1963.

Ameiva undulata stuarti Smith, Proc. Biol. Soc. Washington, 53:55-56, 1940 [Holotype: USNM 108601. Type Locality: Palenque, Chiapas, México. Collector: H. M. Smith]. Stuart, Proc. Biol. Soc. Washington, 55: 146, 1942. Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):50-51, Fig. 1b, Pl. Ib, 1946. Smith and Taylor, U. S. Natl. Mus. Bull., 199:173, 1950.

Ameiva undulata amphigramma Smith and Laufe, Trans. Kansas Acad. Sci., 48(3): 338-344, 1945 [Holotype: FMNH 100020. Type Locality: San Andrés Tuxtla, Veracruz, México. Collector: H. M. Smith]. Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):43-47, Pl. Ic-Id, 1946. Smith and Taylor, U. S. Natl. Mus. Bull., 199-172, 1950.

Ameiva undulata gaigeae Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):37-39, Fig. 1c, Pl. IIc, 1946 [Holotype: FMNH 100030. Type Locality: Progreso, Yucután, México. Collector: H. M. Smith]. Smith and Taylor, U. S. Natl. Mus. Bull., 199:172, 1950. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 122:77, 1963.

Ameiva undulata podarga Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):40-43, Fig. 1d, 2a, 1946 [Holotype: FMNH 100050. Type Locality: 7 mi. W Victoria, Tamaulipas, México. Collectors: H. M. Smith and D. H. Dunkle]. Smith and Taylor, U. S. Natl. Mus. Bull., 199:172, 1950.

Ameiva undulata dextra Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):54-59, Fig. 2c, 1946 [Holotype: FMNH 100080. Type Locality: nr. Rincón, Guerrero, México. Collectors: E. H. Taylor and H. M. Smith]. Smith and Taylor, U. S. Natl. Mus. Bull., 199:173, 1950.

Ameiva undulata sinistra Smith and Laufe, Univ. Kansas Sci. Bull., 31(2):59-62, 1946 [Holotype: FMNH 100054. Type Locality: Manzanillo, Colima, México. Collector: H. M. Smith]. Smith and Taylor, U. S. Natl. Mus. Bull., 199:174, 1950.

Ameiva festiva miadis Loveridge and Barbour, Bull. Mus. Comp. Zool., 69(7):141, 1929 [Holotype: MCZ 26970. Type Locality: Isla del Maiz Grande, Depto. Zelaya, Nicaragua. Collector: James L. Peters].

Ameiva undulata miadis—Dunn, Proc. Acad. Nat. Sci. Philadelphia, 92:115, 1940. Villa, Rev. Biol. Trop., 15(1):119, 1968. Echternacht, Breviora, 354:5, 1970.

Distribution.—The most widely distributed of the Middle American *Ameiva* (Fig. 17), *Ameiva undulata* occurs from near Las Varas, Nayarit, México, to the vicinity of Quepos, Puntarenas Prov., Costa Rica, on the Pacific slopes. On the Atlantic slopes, the species ranges from Rancho Santa Ana (12.8 km SE Podilla), Tamaulipas, México, to Puerto Lempira, Cabo Gracias a Dios, Honduras, and on more westerly Atlantic slopes of Nicaragua from Corozo, Depto. Nuevo Segovia to Tuli Creek, Depto. Río San Juan. Four specimens (ANSP 15438-41) from Huaunta, Depto. Zelaya, Nicaragua, seemingly document the presence of *Ameiva undulata* on the Caribbean coast of that country (see

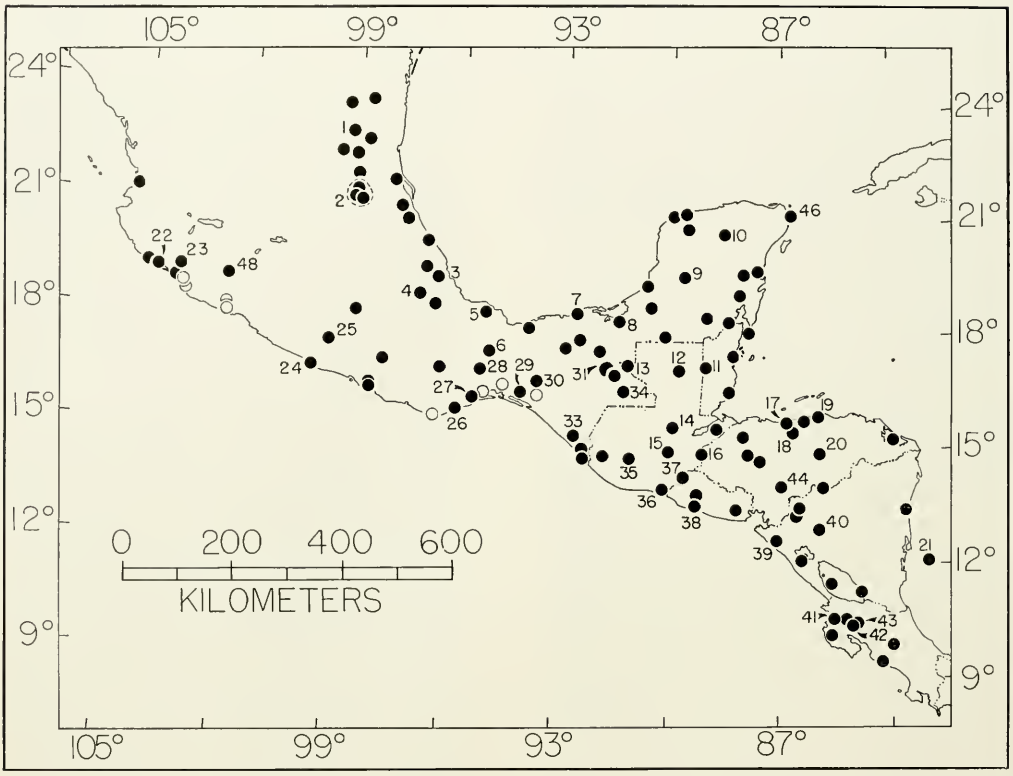


Fig. 17. Map showing locality records of *Ameiva undulata*. To avoid crowding of symbols, some localities have been omitted. Samples used in statistical analyses were (1) Goméz Farías and vicinity, Tamaulipas, México, (2) Tamazunchale and vicinity, San Luis Potosí, México, (3) Tierra Colorado, Veracruz, México, (4) Cuautlapam, Veracruz, México, (5) San Andrés Tuxtla and vicinity, Veracruz, México, (6) Vicinity of Jesús Carranza, Veracruz, México, (7) Frontera and vicinity, Tabasco, México, (8) Tres Brazos and Balchacaj, Campeche, México, (9) Dzilbalchen, Campeche, México, (10) Pisté, Yucatán, México, (11) El Cayo and vicinity, Cayo Dist., British Honduras, (12) Uaxactún and Tikal, Depto. El Petén, Guatemala, (13) Piedras Negras, Depto. El Petén, Guatemala, (14) Canihor, Depto. Alta Verapaz, Guatemala, (15) El Rancho and Finca Bucural, Depto. Progreso, Guatemala, (16) Copán, Depto. Colón, Honduras, (17) La Ceiba, Depto. Atlantida, Honduras, (18) Coyoles Central, Depto. Yoro, Honduras, (19) Trujillo, Depto. Colón, Honduras, (20) Catacamas, Depto. Olancho, Honduras, (21) Isla del Maiz Grande, Depto. Zelaya, Nicaragua, (22) Manzanillo-Pacific Coast Localities, Colima, México, (23) Colima and vicinity, Colima, México, (24) Acapulco and vicinity, Guerrero, México, (25) Chilpancingo and vicinity, Guerrero, México, (26) Chacalapa and vicinity, Oaxaca, México, (27) Tres Cruces, Oaxaca, México, (28) Tolocito, Oaxaca, México, (29) Tapanatepec, Oaxaca, México, (30) Vicinity of Cintalapa, Chiapas, México, (31) Las Tazas, Chiapas, México (51 km E Altamirano), (33) Esquintla, Chiapas, México, (34) Sabana de San Quintín, Chiapas, México, (35) Panajachél, Depto. Sololá, Guatemala, (36) Finca La Trinidad, Depto. Jutiapa, Guatemala, (37) Jutiapa and Finca Mongoy, Depto. Jutiapa, Guatemala, (38) Vicinity of La Libertad, Depto. La Libertad, El Salvador, (39) Chinandega, Depto. Chinandega, Nicaragua, (40) Matagalpa, Depto. Matagalpa, Nicaragua, (41) Hacienda La Norma and vicinity, Guanacaste Prov., Costa Rica, (42) Cañas, Guanacaste Prov., Costa Rica, (43) Tilarán, Guanacaste Prov., Costa Rica, (44) El Zamorano and vicinity, Depto. Francisco-Morazán, Honduras, (46) Isla Mujeres, Quintana Roo, México, (48) Apatzingán, Michoacán, México. Open symbols indicate literature records of specimens not examined for the present study.

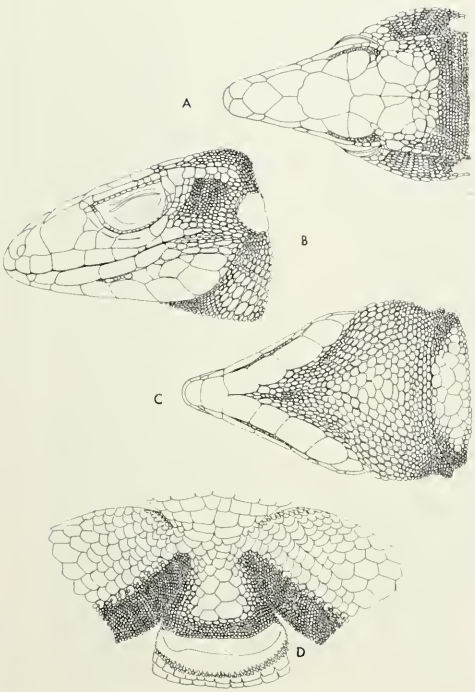


Fig. 18. Head and preanal scutellation of *Ameiva undulata* (KU 94112; Sabana San Quintín, Chiapas, México): (A) Lateral view of head, (B) Dorsal view of head, (C) Ventral view of head, × 1.1. (D) Preanal region, × 1.5.

Remarks). The species is known from Isla Mujeres, east of Quintana Roo, México, and from the Islas del Maiz east of Nicaragua. Gene flow between populations on the Atlantic and Pacific slopes occurs across the Isthmus of Tehuantepec, in the lowlands of eastern Guatemala, and in Honduras and Nicaragua south of the highlands that mark Nuclear Central America. *Ameiva undulata* is generally found at elevations below 1500 m, although there are exceptions (e.g., at Panajachél, Depto. Sololá, Guatemala).

Diagnosis.—*Ameiva undulata* can be distinguished from other Middle American *Ameiva* by the following combination of characters: Central gular scales slightly to greatly enlarged, regular or irregular in arrangement; gradual reduction in size of scales radiating outward from central gular scales; prefrontal scales in contact with postnasal scales; three parietal scales (four if median parietal divided); a transverse row of abruptly enlarged mesoptychial scales; usually eight rows of ventral scutes; a relatively broad middorsal stripe bounded by narrow light stripes which may be lost in adults; no narrow vertebral stripe; lateral pattern emphasizes longitudinal stripes or vertical bars in adults, never spots.

Description.—Maximum observed SVL 129 mm for males, 111 mm for females; supralabials 12-18 (14.1) for males, 12-18 (14.1) for females; infralabials 7-14 (10.2); supraoculars 6-10 (6.4); COF values 2-6 (2.2); COP values 2-14 (10.6); SO-SC values 2-10 (3.8); loreals 2-8 (4.0); nostril in prenasal-postnasal suture; prefrontal in contact with postnasal; median gular

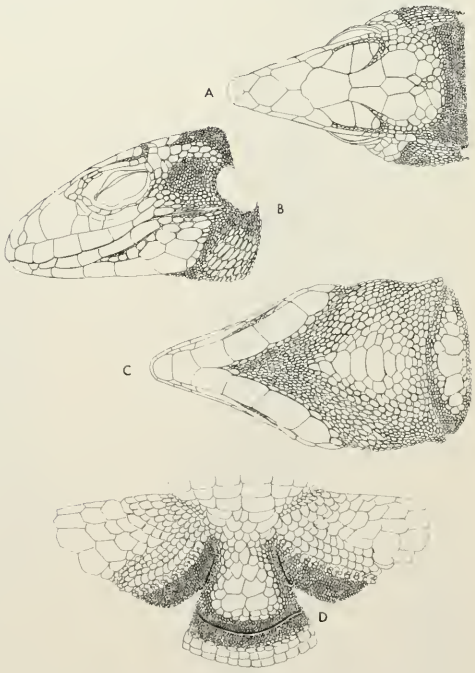


Fig. 19. Head and preanal scutellation of *Ameiva undulata* (KU 26963; 25 km SE Jesús Carranza, Veracruz, México): (A) Lateral view of head, (B) Dorsal view of head, (C) Ventral view of head, × 1.1. (D) Preanal region, × 1.5.

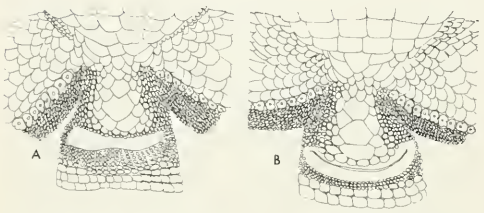


FIG. 20. Preanal Region of *Ameiva undulata* to illustrate two of the pattern types: (A) KU 87417; East of San Andreas de la Cruz, Guerrero, México; Preanal scales in a single row except for paired terminal scales, × 2.7. (B) KU 38232; Chacalapa, Oaxaca, México; Preanal scales in a single row including single terminal preanal, × 1.5.

scales variable in size and orientation; GAB 108-202 (149.5); PV 31-67 (47.4) for males, 33-65 (46.4) for females; PV/GAB 0.21-0.40 (0.32) for males, 0.23-0.43 (0.31) for females; GOR 186-315 (246.0); GAB/GOR 0.44-0.77 (0.61) for males, 0.49-0.74 (0.60) for females; SAT 18-26 (22.3) for males, 18-27 (22.2) for females; total preanal scales 4-13 (7.6) for males, 5-13 (7.5) for females; terminal preanal scales 1-3 (2.0); one (usually) or two rows of enlarged prebrachials; postbrachials enlarged, in one row; preantebrachials in two rows, one row or two rows proximally and one row distally; prefemoral scales enlarged, three to five rows proximally reducing to two (usually) or three rows distally; infratibials enlarged, in two rows, femoral pores 29-48 (37.4) for males, 22-45 (35.0) for females; subdigital lamellae 24-38 (30.2); longitudinal rows of ventral scutes 26-34 (30.1); transverse rows of ventral scutes 8-12 (8.2). For details of scutellation see figures 18-20.

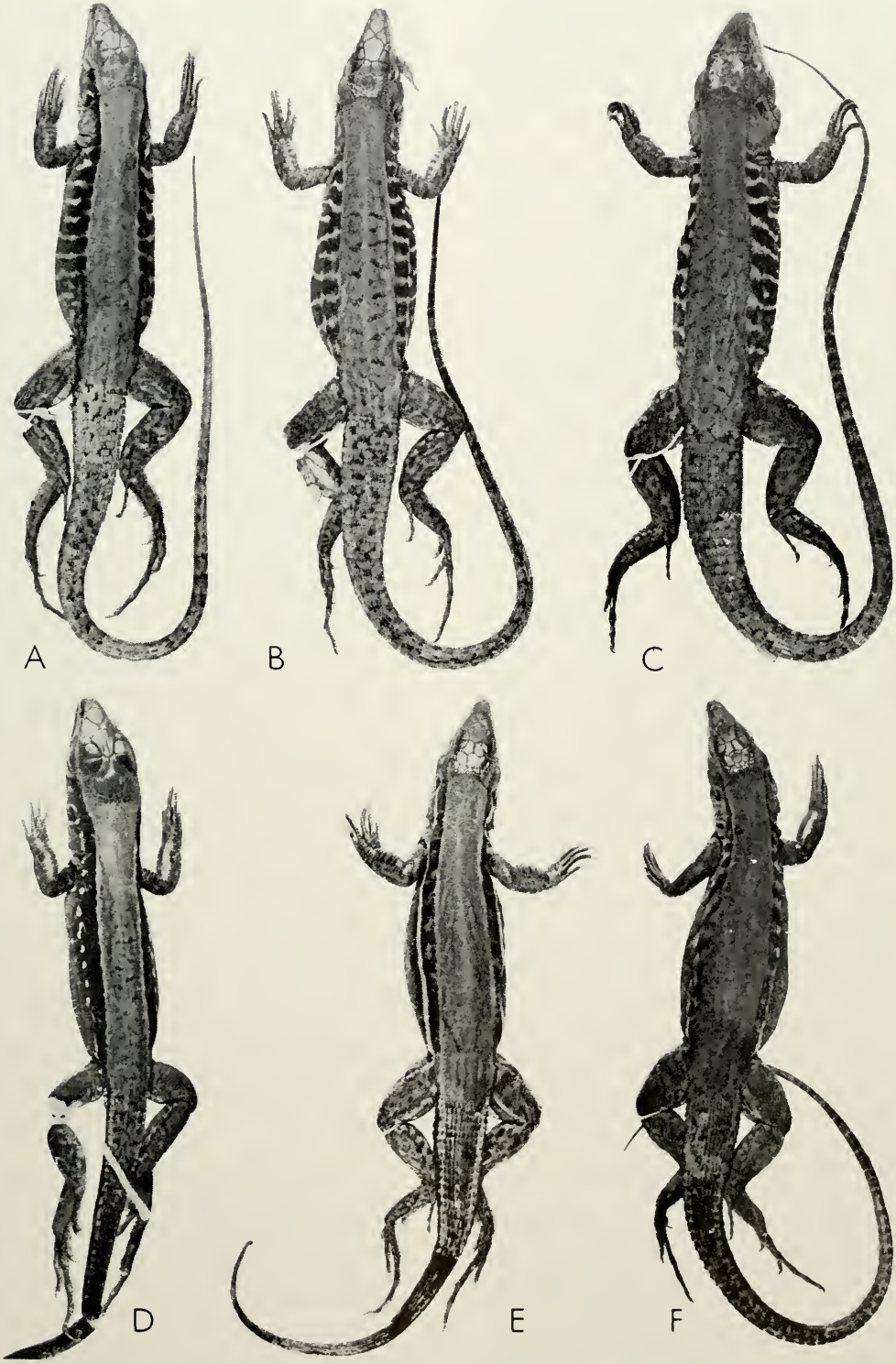
Color and Pattern in Alcohol.— Throughout its broad range, *Ameiva undulata* shows geographic variation in color and pattern unmatched by other Middle American species of *Ameiva* and ontogenetic variation, especially of males, greater than all, except possibly *A. ameiva*. The following description of color and pattern in alcohol, as well as the description of color and pattern in life, is based on specimens of *undulata* from the vicinities of La Ceiba and Trujillo along the north coast of Honduras (Localities 17 and 19, Fig. 21).

Juvenile Males: Top of head brown; side of head black above, grading through brown to gray on supralabials; a white patch beneath and slightly behind eye; ear surrounded by white markings; middorsal field yellowish-brown or greenish-brown with black flecking, bordered laterally by fine white cream-colored dorsolateral stripes which originate above eye and extend well onto tail; dorsolateral dark stripe extending from behind eye to base of tail, velvet black with no light bars or blotches, bounded below by an interrupted white ventrolateral light line originating behind the ear and extending to the groin, thence as an uninterrupted white line well onto tail, ventrolateral dark field gray-brown; dorsal surfaces of limbs mottled black and brown, hind limbs with white spots above; white postfemoral stripe joining caudal extension of ventrolateral light stripe; tail brown with black flecks above; ventral surfaces immaculate or blue-gray.

Through ontogeny (Fig. 21) the dorsolateral light stripe disappears or is retained only on the anterior half of the body. The ventrolateral light stripe is usually lost entirely. Light blue vertical bars appear on the flanks, extending from the border of the middorsal field or near it to or nearly to the enlarged ventral scutes. Shorter bars and blotches may appear between the primary bars. The light spots around the ear are lost and the venter may become light blue

▷

FIG. 21. Ontogenetic change in pattern of *Ameiva undulata* from northern, coastal Honduras. Males: (A) KU 101247, SVL 71 mm; (B) KU 101238, 92 mm; (C) KU 101237, 110 mm. Females: (D) KU 101242, 39 mm; (E) JRM 2318, 88 mm; (F) JRM 2554, 109 mm. Small males resemble small females as exemplified by KU 101242 (D above).


A
B
C
D
E
F

overall except for black patches in the lateral-most scales and on the enlarged plates on the anterior surface of the femur. Traces of red pigment are visible in the gular region of some large males.

Females: Juvenile females are similar to juvenile males. Through ontogeny, females generally retain the juvenile pattern, except that the dorsolateral light stripe may be lost on the posterior one-half of the body and regularly spaced light brown blotches appear in the dorsolateral dark field (Fig. 21).

Color and Pattern in Life.—The following is based on field notes and color photographs of *Ameiva undulata* collected during July, 1967, near La Ceiba and Trujillo on the north coast of Honduras.

Adult Males: Top of head gray-brown to light brown; middorsal field gray-green on neck becoming bright leaf-green on shoulder and extending one-half to two-thirds length of trunk, then becoming golden-brown on posterior part of body; entire middorsal field irridescent in sunlight; dorsal surface of tail gray-brown with black flecking; middorsal field from shoulder to tail lightly to moderately blotched with black which sometimes appear paired; remnant of dorsolateral light stripe cream, if present, and only visible on anterior two-thirds of body; lateral pattern of seven to ten vertical blue-white or greenish-white bars which may touch middorsal field but which usually are separated from it and which taper so that they are wider than or equal to the interspaces dorsally but much narrower than interspaces ventrally; short blue bars extending upward between the prominent lateral bars, sometimes connecting with them; lateral ground color black above (in area of dorsolateral dark field of juveniles), reddish-brown below. Some individuals retain a remnant of the cream-colored ventrolateral light stripe so that the dorsolateral dark field may be defined. Dorsal surfaces of limbs brown with indistinct black mottling; ventral coloration of limbs, body and tail blue-white with black flecking and blotches, especially on the hind limbs and laterally on the body; chin, gular region and neck range in color from white to brick red with no indication of yellow pigmentation.

Adult Females: Dorsal pattern similar to that of males except that cream-colored dorsolateral light stripes usually are retained; dorsal coloration similar to that of males but several shades darker overall; ventrolateral light stripe cream, continuous, broken or broken anteriorly, entire posteriorly; dorsolateral dark field black with brown or cream blotches, each wider than or equal to width of interspaces; ventrolateral field brown or gray-brown with darker mottling; dorsal surfaces of limbs as for males; ventral surfaces immaculate or with slight bluish tint laterally and on hind legs. Females lack the bright vertical bars on the flanks, never show reddish pigment on the ventral surfaces of the head and neck and never develop blue ventral coloration as markedly as do males.

Geographic Variation.—The following samples were removed during STP analysis of sexually dimorphic characters because of inadequate sample sizes: For characters of males, samples 3, 9 and 48; for characters of females, samples 7, 9, 23, 25, 26, 34, 38, 46 and 48. In addition, sample 3 was removed in the analysis of number of loreals of females and both 3 and 22 were removed in the analysis of SO-SC values of both sexes, again for reasons of inadequate sample size.

The most obvious patterns of geographic variation for meristic characters of *Ameiva undulata* are clinal trends along the northeast and northwest coasts of México and along the Pacific coast of Middle America from the Isthmus of Tehuantepec to Nicaragua and Costa Rica (Fig. 22). In some cases one sample along such a cline is "out of phase,"

interrupting what otherwise is a rather smooth trend. Such samples are indicated in parentheses in the following account.

Those characters showing an increase in sample means from Tamaulipas to the Isthmus of Tehuantepec include number of supraoculars (2), number of paravertebral granules of males, number of paravertebrals of females (3), total preanal scales of males, total preand scales of females (4) and number of femoral pores of males. Shorter clines in the same direction, but involving only samples 1 through 3 or 4 are apparent for PV/GAB of males and SAT of males (the size of sample 3 is too small for inclusion in the analysis for both characters), as well as number of femoral pores of females. The cline for total preanal scales of males and of females extends southward across the isthmus and thence eastward along the Pacific coast as far as locality 33 for males and locality 36 for females. Two characters, COF values and number loreals, show clinal increases from north to south across the isthmus and along the coast to varying degrees. For both characters, lowest mean values are for sample 5. COF values increase through samples 28 and 29 and through samples 6, 30 and 33 to 36. The number of loreals increases through samples 28, 27 and 26 and through samples 28, 29 and 30. Mean numbers of supraoculars show the same trans-isthmian pattern as COF values, but in the opposite direction and with the lowest value at sample 35, not 36. GAB increases from locality 5 through 28 and 29 or 6 and 30 to 33 and 36.

Decrease in mean values from Tamaulipas to the Isthmus of Tehuantepec is notable for the number of supralabials of females. Shorter clines in the same direction but involving only samples 1 through 3 or 4 are apparent for GAB and GAB/GOR of males (sample 3 is too small for inclusion in the analysis of GAB/GOR of males) and number

Fig. 22. Major patterns of geographic variation in *Ameiva undulata*. Arrows represent geographical trends involving several characters. Samples on one side of the heavy, dashed line differ from adjacent samples on the other side of the line in a statistically significant manner for five or more characters but do not differ in such a way from adjacent samples on the same side of the line. See text for further elaboration.

of subdigital lamellae. Both COP and SO-SC values increase from south to north across the isthmus and a west to east and northeast increase is noted for SO-SC values.

Northwest to southeast clines are apparent along the south coast of México also. Characters showing increased sample means from Colima to the Isthmus of Tehuantepec or at least to the vicinity of Chacalapa, Oaxaca (Sample 26) include number of paravertebral granules of males and of females, PV/GAB of males and of females, total preanal scales of females and SAT of males (inadequate sample size precludes inclusion of sample 48 in analysis of these characters). Although the clinal trend terminates at the isthmus for the other characters mentioned, that for total preanals of females continues along the Pacific coast to locality 36 in Guatemala. A short trend in the same direction is noted for number of transverse rows of ventral scutes from localities 22 and 23 through 48 to 24 and 25.

Trends along the same coast, but showing a decrease in sample means from Colima to the Isthmus of Tehuan-

tepec are noted for number of supralabials of males (sample 48 excluded from the analysis) and females (samples 26 and 48 excluded), number of infralabials, GAB/GOR of females, number of terminal preanals and number of subdigital lamellae. These trends generally involve only coastal samples (samples 22, 24, 26, 27 and 29), but include inland samples (samples 23, 25 and 48) for supralabials of males and total number of infralabials.

A number of characters show clinal tendencies for increase or decrease in sample means between Nicaragua or Costa Rica and localities 33, 37 and especially 36 to the northwest. There is a marked tendency for clines to either begin or end in the area of southeastern México and southern Guatemala with no clines running through to the southeast or northwest along the coast. Numbers of supraoculars show an increase from sample 40 ($\bar{x} = 6.13$) in Nicaragua to sample 36 ($\bar{x} = 9.97$) in Guatemala, at which point there is an abrupt decrease in sample mean and a clinal increase from sample 33 ($\bar{x} = 6.28$) to sample 5 ($\bar{x} = 6.70$) on the Gulf side of the Isthmus of Tehuantepec in México. Samples 34 (Chiapas) and 35 (Guatemala) are significantly different from the nearest samples to the east in Guatemala for this character, but sample 36 (Guatemala) is not significantly different from sample 33 (Chiapas). A similar trend for increase is noted between sample 39 ($\bar{x} = 2.07$) in Nicaragua and sample 37 ($\bar{x} = 2.29$) in Guatemala for COF values. Sample 36 ($\bar{x} = 3.77$), located just west of sample 37, is significantly different from it and is the end of a cline beginning at sample 5 ($\bar{x} = 2.13$) and which progresses across the Isthmus of Tehuantepec through samples 28 and 29 or samples 6, 30 and 33. Samples 33 and 36 have very high mean values for COF and are statistically isolated from samples to the north. Femoral pore means for both males and females also show increases from sample 40 to sample 37, but the trend may be traced from samples 41, 42 and 43 in Costa Rica as well. For this character in females the cline continues to sample 15 and may also be traced from the Costa Rican samples or sample 40 in Nicaragua through samples 39 and 44 to sample 16 in western Honduras. The number of supralabials of males increases from sample 37 north and westward to sample 29, and GAB/GOR for females increases from sample 37 to sample 33 and from sample 15 to sample 33, both trends running to the west or northwest. Mean numbers of subdigital lamellae increase from samples 20 and 44 through samples 38 and 37 to sample 36 on the coastal plain of Guatemala and to sample 33 by way of samples 15 and 35. Total number of preanal scales of females follow the same trend. These two characters are the only ones involved in clines running through the area of samples 36 and 37. Mean numbers of supralabials of females increase from west to east, beginning at sample 30 and terminating at samples 14 and 37 by way of samples 33, 35 and 15. Sample 36 ($\bar{x} = 13.5$), with a mean for this character lower than that of sample 30 ($\bar{x} = 13.6$) is not part of the trend.

Mean numbers of paravertebral granules of males and of females and PV/GAB of females show trends for increase from sample 40 in Nicaragua or sample 20 in Honduras southwestward and along the Pacific coast to sample 36 in Guatemala. With respect to number of paravertebrals of females, sample 36 is significantly different from sample 37. For both number of paravertebrals of females and PV/GAB of females, the cline may be traced to either sample 36 or sample 15 in Guatemala.

Mean SO-SC values and mean number of loreals show increased values from north to south along a line between sample 9 on the Yucatán Peninsula and samples 37 and 38 in south-

eastern Guatemala and El Salvador, respectively.

There seems to be a trend toward increase in mean numbers of paravertebral granules of females, GAB/GOR of females and total number of preanal scales of males from sample 8 in southwestern Campeche through sample 10 in Yucatán to sample 46 on Isla Mujeres. There is a similar trend beginning at sample 7 in Tabasco and terminating at sample 10 for mean numbers of femoral pores of males. For all of these characters, however, sample 9 in central Campeche (Dzilbalchen) is too small for meaningful comparison ($n = 3$) where females are concerned and such trends might owe their existences to lack of data from this locality. A clinal decrease from sample 8 through sample 9 and 10 to sample 46 is apparent for mean number of rows of transverse ventral scutes. An increase along the same line is noted for mean number of loreals.

Most samples differ from adjacent samples in a statistically significant manner for at least one character. For purposes of this discussion, a character judged sexually dimorphic would count as two characters because separate consideration is given to males and females. If, for example, two samples were significantly different with respect to number of femoral pores of males and females, they would be said to differ significantly for two characters, not one. Viewing all characters at once gives one the impression that each sample is more-or-less statistically isolated from its neighbors. Although this may be true, it renders analysis and formation of meaningful generalizations extremely difficult. However, if only pairs of samples differing statistically by (arbitrarily) five or more characters are examined, some interesting patterns emerge. These are discussed below. It must be emphasized that comparisons are, in most cases, being made only between *adjacent* samples. Two samples adjacent to one another in Honduras may be statistically different from one another on the basis of one or more characters, but neither may differ from a sample in, for example, northern México. Of course, the opposite is also possible.

The population of *Ameiva undulata* on Isla del Maiz Grande (sample 21) differs from samples 42, 43 and 44 for five characters each, from samples 39 and 40 six characters each and from sample 20 for ten characters. With the exceptions of samples 40 and 41, which differ from each other for five characters, none of these mainland samples differ from adjacent samples among those mentioned by more than four characters. This strongly emphasizes the divergence of the *Ameiva* on Isla del Maiz Grande from the nearest mainland populations, or at least from the available samples of those populations, and is indicated by the heavy, dashed line in figure 22. Although sample 20 differs from sample 21 for twice or more the number of characters separating sample 21 from other mainland samples, there is still little basis for concluding that *A. undulata* on the Islas del Maiz were derived from elsewhere because the Honduranian population from which sample 20 was drawn may have been modified itself through introgression of characteristics of populations to the north and west (samples 17, 18 and 19).

The latter three samples represent a population quite distinct from neighboring samples on the basis that none of the three differ among themselves by more than one character (17 and 18 differ from 19 for SO-SC values; other characters show non-significant differences among sample means), but all differ from other nearby samples by more than five characters (see Fig. 22). Samples 16, 20 and 44, which encircle samples 17, 18 and 19, do not differ among themselves, but all show considerable divergence from samples 17, 18 and 19 for meristic and, as will be

discussed later, color and pattern characters. Samples 17, 18 and 19 differ from sample 11 (El Cayo and vicinity, British Honduras) for only three, one and one characters, respectively. Sample 16, on the other hand, differs from sample 11 for four characters, none of which are among those few which distinguish sample 11 from samples 17, 18 and 19.

Samples 9-16, 31, 34, 35, 37, 38 and 46 all show statistically significant differences involving fewer than five characters when compared among themselves with respect to adjacent samples. However, sample 8 differs from samples 12, 13, 31, 33 and 34 for ten, ten, eight, ten and seven characters, respectively. In addition to sample 8, sample 31 differs from samples 6, 7, 30, 33 and 35 for six, seven, nine, ten and nine characters respectively. Sample 33, in addition to differing from samples 8 and 31 by more than five characters, differs from samples 34 and 35 by six and seven characters, respectively. Sample 36 differs from samples 15, 35 and 37 for seven, eight and seven characters, respectively. Samples 8, 7, 6, 30, 33 and 36 constitute a series of localities beginning in the Tres Brazos-Balchacaj area of Campeche, progressing west along the Gulf coast and thence south across the Isthmus of Tehuantepec and eastward along the Pacific slopes to the vicinity of Finca La Trinidad, Depto. Jutiapa, Guatemala. These samples, as indicated above, all differ from adjacent more inland samples to the south, east or north by five or more characters. If a line is drawn to emphasize the divergence of these "peripheral" samples from the other, more inland, samples (Fig. 22), none of the samples falling within the curvature of the line differ from adjacent samples by as many as five characters with the exception of sample 15, which differs from sample 35 for six characters.

Sample localities from the northern Gulf region of México (samples 1-5) are isolated from sample localities along the southwest Pacific coast (samples 22-27, 48) by the Mexican Plateau. In general, however, samples on the one coast differ for five or more characters only from the most distant samples on the other coast. For example, sample 1 (Tamaulipas) differs from sample 27 (south-central Oaxaca) for seven characters, but differs from sample 22 (Colima) for only three characters. Sample 5 (San Andrés Tuxtla and vicinity, Veracruz) differs from sample 27 for only four characters, but differs from sample 22 for nine. Samples 1-5 and 22-27, 48 do not differ from adjacent samples on the same coast by more than two characters, with the exception of samples 25 and 26, which differ for four characters.

Sample 27 (Tres Cruces, Oaxaca), however, seems to be strongly divergent from adjacent samples to the east. Sample 27 differs from samples 6, 28 and 29 for ten, six and eight characters, respectively. This, coupled with the isolation afforded by the Mexican Plateau, is the basis for separating off the samples from the Pacific slopes of México northwest of the Isthmus of Tehuantepec as shown in figure 22.

The groupings of samples set apart according to the method just described fits well with the general pattern of clinal trends discussed earlier. There is also a generally good fit by these groupings with the placement of highland regions with elevations above 1500 meters, an elevation above which *Ameiva* rarely occur in Middle America.

Using the 14 samples (8, 15-21, 27, 31, 33, 35, 37 and 44) which were found to differ from adjacent samples by five or more characters, it is possible to arrive at some idea of which characters are most discriminatory in distinguishing adjacent samples. The 14 samples were compared with adjacent samples to give 68 different comparisons. It was found that in 53 per cent of these comparisons (36 out of the possible 68),

mean GAB differed in a statistically significant manner. GAB is apparently the primary meristic indicator of sample differences, followed by GOR (43 per cent of the comparisons), SO-SC values (31%), number of subdigital lamellae (31%) and COP values (29%). All other characters were involved in 26 per cent or less of the comparisons each. Two characters, number of supralabials of males and number of transverse rows of ventral scutes, were found not to distinguish any of the 68 pairs of samples compared. All five of the characters which seem most important in this respect do not appear together in distinguishing two adjacent samples, but they do appear in groups of 2, 3 or 4 in various comparisons. GAB and GOR, as might be expected, occur together most often in distinguishing pairs of adjacent samples, appearing in 26 of the 68 comparisons (38%). GAB and number of subdigital lamellae occur together in distinguishing 15 pairs among the 68 (22%), whereas GAB and SO-SC values, and GAB and COP values both occur together in 14 of 68 comparisons (20%). Other combinations of the five characters taken two at a time occur less frequently.

The condition of the preanal scales of *Ameiva undulata* can be analyzed in a number of ways. Two of these, the total number of preanals and the number of terminal preanal scales have been defined and discussed with respect to STP analysis. These characters, along with a third which combines the two, warrant further discussion.

For STP analysis, the number of terminal preanal scales was coded 1, 2 or 3, indicating one, two or three scales in the terminal position. An inherent weakness in this system is that a sample mean or range gives no indication of the actual frequency distribution of single, double and triple terminal preanals in the sample. A sample of two individuals, one having one terminal preanal, the other having three, would have the same mean number of terminal preanals as another sample of two individuals where each animal had two terminal preanal scales. This is an oversimplification complicated by larger sample sizes. Even statistics, such as standard deviation, are of little help in visualizing the frequency distribution. For this reason, the number of terminal preanal scales was coded so that three terminal preanal scales received the same value as one. This system has some validity in that only scales in the midline are being compared. Individuals having two terminal preanals continue to receive a code value of two. If this is done, most samples still have a mean number of terminal preanals near or approaching 2.00, but certain samples have much lower values. The lowest of these are samples 1 ($\bar{x} = 1.67$), 8 (1.60), 17 (1.67), 22 (1.42), 23 (1.61), 25 (1.76), 26 (1.66), 27 (1.33) and 48 (1.78). Means of other samples ranged from 1.80 (sample 9) to 2.00 (many samples). It will be noted that most of the low sample means are encountered in samples 22-27 and 48 between Colima and Tres Cruces, Oaxaca, in México. Sample 24, consisting of 14 individuals each with two terminal preanal scales, does not fit the pattern.

Coupled with the number of terminal preanal scales is the pattern of these scales. They may be (A) mostly (>50%) single (Fig. 20B), (B) mostly paired, (C) single except the terminal scales paired (Fig. 20A), or (D) mixed. The latter category includes individuals not fitting into any other category if the single or paired condition is based on three or more scales or pairs of scales in a row. Most individuals of *Ameiva undulata* fall into class C (71.6%; n = 1003), whereas fewer are referable to classes A (18.2%), B (4.5%) and D (5.7%). Two series of samples, however, show marked deviation from this distribution. If samples 22-27 and 48, from the Pacific slopes of México north and west of the Isthmus of Tehuan-

tepec, are combined, there are about equal numbers of individuals referable to classes A (33.9%), B (27.3%) and D (30.6%), but only 8.3 percent are referable to class C (n = 121). Individual lizards in samples 41-43 from Costa Rica are distributed as follows: class A (44.2%); class B (3.9%); class C (35.1%); class D (16.9%) (n = 77). On the basis of this character alone samples 41-43 differ markedly from samples to the north (samples 39-40 in Nicaragua), but the divergence of samples 22-27 and 48 parallels that noted for number of terminal preanal scales and appears to reinforce the evidence for a break in gene flow between populations of *undulata* east and west of a line drawn between sample 27 and samples 28 and 29. If samples 21-27, 41-43 and 48 are removed, the distribution of individuals in the remaining samples becomes: class A (13.4%); class B (1.1%); class C (84.6%); class D (0.9%) (n = 805).

Another character not analyzed by STP, but warranting further mention is the pattern of the median gular scales. Median gular scales may be either irregular in arrangement or oriented longitudinally in a more-or-less regular row. If irregular, they are usually at least slightly enlarged (39.0%; 404 of 1026 individuals), although a few individuals have midgular scales no larger than surrounding scales (0.4%). If longitudinally oriented and enlarged, they may be paired (2.1%), in a row of single scales (34.8%) or mixed paired and single (23.1%; at least three scales or pairs of scales in a row were deemed necessary to classify a lizard as having longitudinally oriented scales). Samples 3-8, 15, 22-30, 33, and 35-36 are made up of individuals more than 70 percent of which have enlarged, longitudinally oriented gulars. Samples 5, 7, 8 and 28 contain only such individuals. These sample localities are distributed along the Gulf coast of México east and west of the Isthmus of Tehuantepec from northwestern Veracruz to the Tres Brazos-Balchacaj region of Campeche, across the Isthmus and along the Pacific coast from Colima to southeastern Guatemala (Fig. 17). Samples 9-14, 17-19, 31 and 34 from the Yucatán Peninsula, eastern México, northern Guatemala and northern Honduras are composed of individuals more than 70 percent of which have enlarged, irregularly arranged gulars. Samples 13 and 34 consist of only such individuals.

These patterns are generally reflected in the lines between adjacent samples depicting significant differences involving five or more characters (Fig. 22). Gular pattern tends to place samples 17-19 from northern Honduras with samples from northern Guatemala and Yucatán Peninsula. The line separating samples 6-8, 30 and 33 from samples 12-13, 31 and 34 is represented, but samples 15 and 35 are not differentiated with respect to gular scale pattern and these samples do not differ from sample 36. Samples 15, 35 and 36 differ from one another for at least five of the characters analyzed by STP. With respect to gular pattern, sample 36 differs sharply from sample 37 and most other samples to the south and east. Sample 36 contains only one individual out of 30 (3.3%) with irregularly arranged gulars, whereas sample 37 contains 13 of 31 (41.9%) individuals with irregular gular scales.

FIG. 23. Selected geographic variants of color pattern of adult *Ameiva undulata*. (A) KU 101300, male, SVL 126 mm, (B) KU 101301, female, 109 mm, both from Isla del Maiz Grande, Depto. Zelaya, Nicaragua; (C) KU 87409, male, 93 mm, from 5 km E Vista Hermosa, Oaxaca, México; (D) UMMZ 41435, female, 99 mm, from Cuautlapam, Veracruz, México. (E) KU 95645, male, 92 mm, from 3 km E Mapastepec, Chiapas, México; (F) KU 95643, female, 82 mm, from 4.5 km E Mapastepec, Chiapas, México. (G) KU 101260, male, 93 mm, (H) KU 101267, female, 90 mm, both from El Zamorano, Depto. Francisco-Morazán, Honduras.

A
B
C
D
E
F
G
H

Samples 16 (19% with irregularly arranged gulars; n = 16), 40 (20%; n = 15) and 2 (73%; n = 15) stand out as having unusually high or low numbers of individuals with irregularly arranged gular scales relative to adjacent samples. Sample 2 would seem to belong with samples from the Yucatán Peninsula, northern Guatemala and northern Honduras, whereas samples 16 and 40 are more like samples involved in the Isthmus of Tehuantepec "X."

In samples other than those specifically mentioned above, the percentage of irregularly arranged gular scales ranged from 33 to 63.

Discussion of geographic variation in color and pattern over the broad range of *Ameiva undulata* is complicated by the presence of both ontogenetic variation (especially among males) and sexual dimorphism (Stuart, 1942). The magnitude of ontogenetic change encountered is apparent in figure 21, and sexual dimorphism in patterns of adults from selected populations is represented in figure 23. That geographic variation is considerable is also apparent from figure 23. There are two basic pattern types (Stuart, 1942). The first of these is characterized by an emphasis on longitudinal stripes rather than blotches or bars on the flanks, by the small amount of sexual dimorphism evident, and by its restricted geographic range. This pattern type occurs only in samples 7 and 8 of the present study, but it apparently grades into other pattern types to the west and south. Smith and Laufe (1946, Pl. IB) have illustrated an individual exhibiting this color pattern from Tenosique, Tabasco, México. These authors cite specimens having this pattern from Palenque and San Ricardo, Chiapas; Frontera, Teapa and Tenosique, Tabasco; Balchacaj and Tres Brazos, Campeche. I have examined two specimens from San Ricardo, Chiapas (FMNH 106715, male; UIMNH 26157, female). The male has 10 light-colored blotches in the dorsolateral dark field, a pattern not characteristic of the striped forms of *undulata*. Nine males (FMNH 106715; UIMNH 8437, 8439, 30229, 39233-4, 39237-40) from Finca San Bartola, ca 12 mi SW of Cintalapa and near San Ricardo, also show prominent bars and/or blotches on the flanks. The specimens from Finca San Bartola and San Ricardo comprise sample 30 of this study; on the basis of both meristic and pattern characters, this sample is distinct from those to the north. The striped pattern type seems to be restricted to the lowlands of Tabasco, extreme western Campeche and northern Chiapas. The pattern is not unlike that of *quadrilineata* (Fig. 16) of Nicaragua, Costa Rica and Panamá or *chaitzami* (Fig. 27) of eastern Chiapas, México and Guatemala. Some *undulata* having the striped pattern share with *chaitzami* and, to a much lesser extent, *quadrilineata,* the presence of a secondary dark stripe in the middorsal field medial to the dorsolateral light stripes.

The second basic pattern type is characterized by a highly variable pattern of bars and/or blotches on the flanks of adult males often accompanied by loss of the ventrolateral light stripe or its reduction to a series of dashes or spots. However, some adult females, as well as juveniles of both sexes, retain a pattern of longitudinal stripes (Figs. 21, 23). Specimens of *Ameiva undulata* included in samples 4, 6 and 28 possess this pattern type (Fig. 23 C and D; Smith and Laufe, 1946, Plate I C and D). The dorsolateral dark field is retained in both sexes, but the ventrolateral light stripe may be completely or partially lost in adult males such that the ventral border of the dark field is indistinct. The ventrolateral light stripe is usually retained in females. The dorsolateral light stripe, which is usually retained in females may be completely lost in males or retained only anteriorly. In many specimens the middorsal field contains dark patches which lie para-

vertebrally and may be paired. This is especially notable in specimens from sample 6. A characteristic of individuals from these samples is a light stripe with indistinct borders lying in the dorsolateral dark field and extending from the ear to the groin (Fig. 23 C and D). This stripe is usually continuous but, if broken, the interspaces are much narrower than the remnants of the stripe. The stripe is white or blue-white in males, pale brown in females and is narrower and less distinct in females. The ventrolateral field contains vertically oriented bars or blotches on a dark background in adult males. Some males in sample 5 show a tendency for the blotches in the dorsolateral field to be continuous with those in the ventrolateral field. The ventrolateral field of females is mottled. Females in samples 6 and 28 occasionally have a secondary dark stripe between the dorsolateral light stripes and the lighter brown area of the middorsal field, the same as described for individuals from samples 7 and 8.

Adult male *A. undulata* in samples 1 and 2 are similar in pattern to those just described, but the dorsolateral dark field contains a series of large, quadrangular, white or blue-white blotches which are two or three times as wide as the interspaces. These blotches are never fused into a solid stripe. The dorsolateral dark field of females contains similar, but less prominent blotches. The dorsolateral light stripe, which is retained in its entirety in some adult females, terminates at one-half to two-thirds of the distance from occiput to groin in juvenile males and may be present only on the neck in adults.

Adult males from samples 22, 23 and 48 are similar to those of samples 1 and 2, except that the blotches in the dorsolateral dark field may be subequal in width to the interspaces. Samples 24 and 25 contain adult males with dorsolateral blotching as in samples 22 and 23, but also contain some males in which the blotches are fused into a continuous stripe as described for samples 4, 6 and 28. In addition, there is a greater tendency for the dorsolateral light stripe to be retained in males from samples 24 and 25 than in males from samples 22 and 23.

With few exceptions, other samples of *Ameiva undulata* from Pacific drainage localities in México present a variety of lateral patterns ranging from presence of blotches in the dorsolateral dark field and spots, blotches or bars in the ventrolateral field to having the entire flanks barred or a combination of both patterns. No one pattern type prevails among males of any one sample. Adult males in sample 44 (El Zamorano and vicinity, Depto. Francisco-Morazán, Honduras) are unusual in that both males and females possess numerous (12-13 per side) small blotches in the dorsolateral dark field. These blotches are tear-drop shaped, and some extend ventrally (Fig. 23 G and H). This pattern is not apparent elsewhere.

Samples 9-14, 16-19, 21, 34, 39-43 and 46 are characterized by a lateral pattern of white or blue-white bars which extend from the dorsolateral light stripe or just beneath it to or almost to the enlarged ventral scutes (Figs. 21 C and 23 A; Taylor, 1956, Fig. 67). The bars show little or no differentiation into dorsolateral and ventrolateral components. The dorsolateral dark field is usually present in adult males, but it is difficult to define because it grades gradually into the ventrolateral field. In such males the dorsolateral and ventrolateral light stripes are retained only anteriorly and the ventrolateral light stripe may be completely lacking in large adults. Sexual dimorphism is marked. With the exception of those from Isla del Maiz Grande (sample 21), adult females retain a juvenile pattern with the addition of blotches in the dorsolateral dark field (Fig. 21 D-F). Adult females from Isla del Maiz Grande resemble adult males in pattern

TABLE 2.—Total number of lateral bars for some samples of male *Ameiva undulata*. Arranged in descending order according to sample mean.

Sample Number	$\bar{X}$	S.D.	*N*	Range
46	29.7	1.11	7	28-31
12	25.4	3.47	9	20-31
9	24.6	3.58	5	20-28
10	24.3	3.20	14	19-29
34	21.6	1.67	5	20-24
42	21.0	0	4	21
21	20.0	1.95	20	16-23
41	20.0	1.81	12	16-22
43	19.8	1.34	7	18-22
18	19.6	2.25	16	16-23
14	19.5	1.77	8	17-22
13	19.4	1.81	9	16-21
39	18.6	1.78	10	17-22
40	18.3	1.97	6	16-21
17	17.8	1.28	8	16-20
19	16.8	1.92	5	15-20

(Fig. 23 A-B), but not in color. The total number (sum of number on both sides) of vertical bars of males varies considerably among these samples (Table 2). The largest sample means are those of samples on the Yucatán Peninsula and Isla Mujeres. The sample from Isla Mujeres (sample 46) has a mean of 29.7, the largest recorded. Lowest sample means occur in the two northern coastal samples from Honduras (samples 17 and 19), with means of 17.8 and 16.8, respectively. Males from samples 9-14, 17-19, 34 and 46 may be differentiated from barred males from other samples in that they have little or no secondary spotting or blotching between the bars in the ventrolateral field. Taken as a whole, barred males from other samples have such markings to a greater degree, although individuals from these samples may show few secondary markings.

The general ontogenetic changes exhibited by the barred populations of *Ameiva undulata* are illustrated in Figure 21. Neill (1961, 1965), reported that young *undulata* from parts of British Honduras lack lateral light stripes, the ontogenetic progression being from unstriped hatchlings through light-striped subadults to barred adults. Presumably this refers to ontogeny of males only. Neill (1965) also called attention to two small specimens (MCZ 71623-24) from Augustine, Cayo Dist., British Honduras. MCZ 71623 has four light lines on each side, whereas MCZ 71624 has three. Augustine is in the ecologically distinctive Mountain Pine region of British Honduras.

Among samples of *Ameiva undulata* there is considerable geographic variation in amount of dark pigment scattered as flecks or blotches in the middorsal area. These dark markings usually take the form or more-or-less paired or alternating, paravertebral spots, although in heavily pigmented specimens a reticulate pattern may be evident. The latter is especially evident in specimens from Isla del Maiz Grande (Fig. 23 A-B). Both sexes may exhibit such markings. Although they are sometimes evenly distributed, the markings are often restricted to or heaviest on the posterior one-half or two-thirds of the back. I have not attempted to quantify this aspect of pattern but feel justified in making the generalization that the samples along the Pacific slopes from southeastern Chiapas, México through El Salvador (samples 33, 35-38) and northward into Honduras south of the northern coastal ranges (samples 16, 20 and 44) are the most heavily marked of the mainland populations sampled. Specimens from Isla del Maiz Grande (sample 21) have very heavy middorsal marking, as noted above, but this marking takes a different form, appearing to be a continuation of the lateral pattern. Samples 39 and 40 are variable with respect to this character and samples 41-43 show very light markings. A few specimens of *Ameiva undulata* are available from the Meseta Centrale of Costa Rica. This population was named by Cope (1894) as *Cnemidophorus*

Fig. 24. *Ameiva undulata* (Holotype of *Cnemidophorus amivoides* Cope; AMNH 16316) from La Carpintera, Cartago Prov.?, Costa Rica, illustrating the heavy blotching in the middorsal area and the divided interparietal; a male, SVL 64 mm.

amivoides (see Remarks). These specimens all show a high degree of marbling or blotching in the middorsal region (Fig. 24), a pattern sharply divergent from that of other populations of *undulata* at the southern end of its range. Further study of this population is desirable. Samples other than those specifically mentioned above show variable markings from light to moderate in extent.

There is little geographic variation with respect to color other than that directly associated with pattern. Studies of such variation are hampered by a paucity of good color-in-life descriptions. Such descriptions are available for samples from Michoacán, México (Duellman, 1961), the Yucatán Peninsula (Maslin, 1963; Duellman, 1965a), British Honduras (Neill, 1965) and Chiapas (Alvarez del Toro, 1960). Other descriptions have been gleaned from my own field notes and those of William E. Duellman.

The most striking aspect of geographic variation in color has to do with color in the gular region of adult males. As noted for *Ameiva festiva* and *quadrilineata*, the gular coloration of males may be associated with reproductive condition. In many specimens throughout the range, gular coloration (and ventral coloration in general) is white or cream. In other specimens, the entire venter is pale blue. A number of individuals, however, show either red or yellow pigment in the gular region and over the anterior part of the chest and ventral surfaces of the forelimbs. The red coloration ranges from orange or brick-red to scarlet. The yellow pigment is a bright lemon yellow. Whether one color precedes the other in a dynamic system of change is not known, but I have observed no specimens intermediate in coloration. The specimens upon which this discussion is based were collected during June, July or August between 1959 and 1966 by a number of collectors. Yellow pigment has been observed to the exclusion of red at only three localities in México: along the Río Frio, Tamaulipas; Finca Orizaba, Chiapas; and Tapanatepec, Oaxaca. At some localities, individuals may have either red or yellow pigment in the gular region. Thus, Duellman (1965a) reported that about half of his sample from Pisté, Yucatán had orange throats, whereas half had yellow throats, corroborating an observation by Maslin (1963). Other localities from which both colors have been reported are Felipe Carillo Puerto, Quintana Roo (Duellman, 1965a), British Honduras (Neill, 1965) and the Tepalcatepec Valley of Michoacán (Duellman, 1961). Specimens from a number of other localities in Veracruz, Tabasco, Campeche, Yucatán, Quintana Roo, Chiapas, Jalisco, Honduras and Isla del Maiz Grande, Nicaragua had only red-throated individuals.

There seems to be some geographic variation in coloration of the middorsal area. This area is iridescent moss-green anteriorly grading to yellowish-brown posteriorly in specimens collected by me at La Ceiba, Coyoles and Trujillo, Honduras (samples 17-19, respectively). It is reported as "olive" for specimens from British Honduras (Neill, 1965) and Chiapas (Alvarez del Toro, 1960). Specimens from the Tepalcatepec Valley, Michoacán (Duell-

man, 1961); Pisté, Yucatán (Maslin, 1963); along the Río Frio, Tamaulipas; 16 km. SW Frontera, Tabasco; Mapastepec, Chiapas; vicinity of Melaque, Jalisco; El Zamorano, Depto. Francisco-Morazán, Honduras (personal observation) have brown middorsal pigmentation. Few descriptions of lateral ground color of living lizards are available, but there may be considerable geographic variation for this character as well.

Ecological Notes.—Despite its broad range and relative abundance in many parts of that range, there have been no thorough ecological investigations of *Ameiva undulata.* Literature on this subject is limited to miscellaneous observations. Thus, Stuart (1951) found *undulata* altitudinally distributed to about 2000 m in the "moderately humid" region near Panajachél, Depto. Sololá, Guatemala, but commented that in more moist areas the altitudinal limit is reached about 400 m lower. Elsewhere, the species seems to occur below 1500 m, and its vertical distribution may be limited to below the level of occasional frosts (1200-1500 m, depending upon humidity), a factor considered by Stuart (1966) to be of possible biological significance.

Throughout most of its range, *Ameiva undulata* is found in forest or forest-edge situations (Alvarez del Toro, 1966; Duellman, 1965a; Echternacht, 1968; Rand, 1957; Stuart, 1935, 1950, 1954b, 1958) or, in drier regions, dense thickets and scrub (Maslin, 1963; Schmidt and Stuart, 1941; Stuart, 1948).

Stuart (1950), Duellman (1966), and Echternacht (1968) commented on the sciophilic nature of *Ameiva undulata,* although I pointed out that even the more shade-tolerant species of *Ameiva* may utilize open areas in the absence of competition from more heliophilic macroteiids like *Cnemidophorus.* Stuart (1950) reported *undulata* to be abundant in the grassland and riparian habitats of Depto. Alta Verapaz, Guatemala, and Echternacht (1968) found the species to be common in open situations near Panajachél, Depto. Sololá, Guatemala. Although the lizards shun the open beach, I found the species occupying clearings, paths and other open areas as well as thickets and piles of debris in the coconut groves of Isla del Maiz Grande, Depto. Zelaya, Nicaragua. In northern Honduras, western Nicaragua, northwestern Costa Rica, and in those parts of México with which I am familiar, *undulata* occurs in shaded areas; the more open parts of the habitat are occupied by various species of *Cnemidophorus.*

Virtually nothing has been reported on the reproduction of this species of *Ameiva.* As I have remarked elsewhere, research on this topic may reveal the sequence and basis for changes in gular pigmentation of adult males.

Stuart (1958) collected 56 juveniles and only four adults of *Ameiva undulata* at Tikal, El Petén, Guatemala, between February and May, 1956, but he cited a collection made by Gosner at the same locality at unspecified dates in 1947 and 1949 that contained a "fine series of adults." This, along with my own observations, suggests that adult and subadult *Ameiva* may have different seasonal activity periods. However, there have been no observations of a quantitative nature to substantiate this.

Remarks.—I have examined four specimens of *Ameiva undulata* (ANSP 15438-15441) from "Wounta" (= Huaunta) Haulover, Depto. Zelaya, Nicaragua. This locality is at least 290 kilometers from other known localities for the species. Duellman (1958) examined three specimens (ANSP 15445-15447) of the snake *Leptodeira annulata rhombifera* Günther from the same locality, far removed from the remainder of the range of the species. Although it is possible that a snake might have been carried to Huaunta by man, it is unlikely that a moderately large, active lizard could be so transported. *Ameiva undulata* shuns deep forest, and

it is unlikely to have arrived at Huaunta along rivers from the west, but it is possible that the species exists in isolated or semi-isolated populations along the Atlantic coast of Nicaragua northward. An alternative hypothesis would be that the *Ameiva* and *Leptodeira* populations at Huaunta are relict and that a more careful survey of the region would uncover other such species as well. This part of Central America certainly deserves more attention from biologists than it has received.

Such an explanation does not apply for records of *Ameiva undulata* from Panamá (Brennan and Yunker, 1966). All specimens so reported are *leptophrys*.

Taylor (1956) placed *Cnemidophorus amivoides* Cope from the Meseta Central of Costa Rica in the synonymy of *Ameiva undulata*, and I see no reason to dispute this judgment. I have called attention to the unusual color pattern of specimens from the Meseta Central (Fig. 24), but so few are available that further comment is unjustified at this time.

Dunn (1940a) and Villa (1968) included the population of *Ameiva* on the Islas del Maiz, Depto. Zelaya, Nicaragua (sample 21) in the species *undulata*. The population was described as a subspecies of *festiva* by Barbour and Loveridge (1929a). I have substantiated the assignment of this population to *undulata* (Echternacht, 1970).

Ameiva chaitzami Stuart

Ameiva chaitzami Stuart, Proc. Biol. Soc. Washington, 55:143-145, 1942 [Holotype: UMMZ 90638. Type Locality: "Along Cahabón-Languín trail about 2 km north of Finca Canihor . . . , Alta Verapaz, Guatemala." Collector: L. C. Stuart]. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan No. 122, p. 77, 1963. Echternacht, Breviora, 354: 7, 1970.

Ameiva undulata stuarti—Stuart, Occas. Papers Mus. Zool., Univ. Michigan No. 471, p. 21, 1943.

Ameiva undulata thomasi Smith and Laufe, Univ. Kansas Sci. Bull. 31(2):47-50, Pl. IA, 1946 [Holotype: FMNH 100006. Type Locality: La Libertad, Chiapas, México, near Río Cuilco where it crosses Guatemalan border. Collector: H. D. Thomas]. Smith and Taylor, U. S. Natl. Mus. Bull. 199, p. 173, 1950.

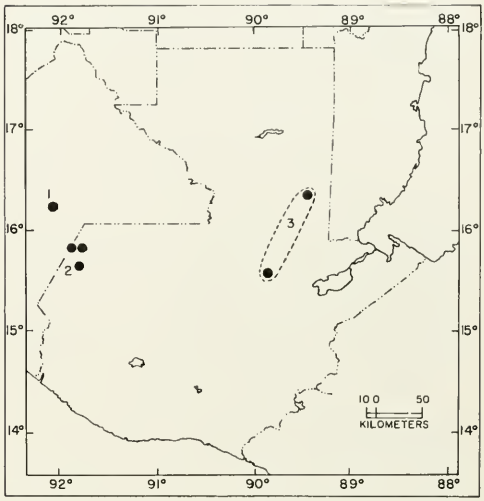


FIG. 25. Map showing locality records of *Ameiva chaitzami*. Samples used in statistical analyses were (1) Comitán, Chiapas, México, (2) Vicinity of San Antonio Huista, Depto. Huehuetenango, Guatemala, (3) combined sample of those specimens originally designated by Stuart (1942) as holotype and paratypes from the Languín-Cahabón road near Finca Canihor, Depto. Alta Verapaz, Guatemala, and specimens from the vicinity of Poptún, Depto. El Petén, Guatemala, later collected by Stuart and identified as *A. chaitzami*.

Distribution.—Known from the valleys of the upper tributaries of the Río Grijalva in Chiapas, México and west-central Guatemala, from along the Languín-Cahabón trail near Finca Canihor, Alta Verapaz, Guatemala, and near Poptún, El Petén, Guatemala (Fig. 25).

Diagnosis.—*Ameiva chaitzami* can be distinguished from other Middle American congeners by the following combination of characters: Small size (maximum observed SVL of males 85 mm, of females 75 mm); central gular scales enlarged, in longitudinal arrangement; gradual reduction in size of scales radiating outward from central gular scales; prefrontal scales in contact with

postnasal scales; three parietal scales (four if median parietal scale divided); a transverse row of abruptly enlarged mesoptychial scales; usually eight transverse rows of ventral scutes; relatively narrow middorsal stripe (mean PV = 37.1); no narrow, well-defined vertebral stripe; usually a dark secondary stripe medial to the dorsolateral light stripes; dorsolateral blotches of males fused to the dorsolateral light stripe such that the latter has a well-defined dorsal border and an irregular ventral border.

Adult male *Ameiva chaitzami* can be distinguished from other *Ameiva* readily on the basis of pattern. Juvenile individuals and females are difficult to differentiate from some *undulata*, especially those from the coastal lowlands of eastern Veracruz, Tabasco, Chiapas and extreme western Campeche, México. However, there are no signs of intergradation or hybridization of *chaitzami* with other species of *Ameiva*. The only *Ameiva* with which *chaitzami* comes in contact is the large form of *undulata* having a color pattern as shown in figure 21, and there is no difficulty in distinguishing the two species.

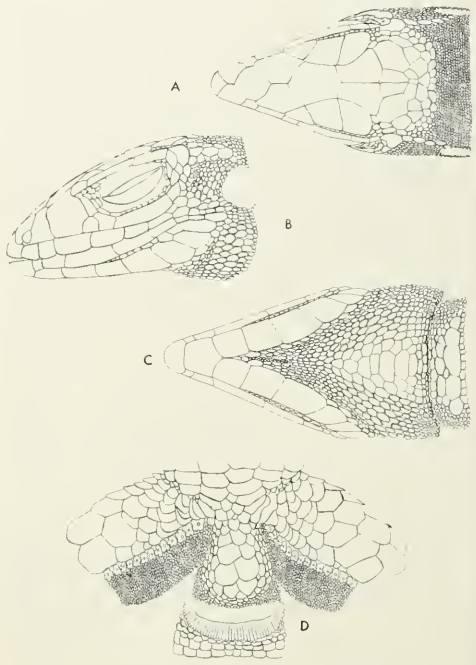


FIG. 26. Head and preanal scutellation of *Ameiva chaitzami* (UMMZ 90643, paratype, from along the Cahabón-Languín trail about 2 km N Finca Canihor): (A) Lateral view of head, (B) Dorsal view of head, (C) Ventral view of head, × 2. (D) Preanal region, × 2.7.

Description.—Maximum observed SVL 85 mm for males, 75 mm for females; supralabials 13-16 (14.2); infralabials 9-13 (10.1); supraoculars 6-8 (6.2); COF value 2; COP value 10-13 (11.6); SO-SC value 2-8 (2.3); loreals 2-4 (3.7); nostril in prenasal-postnasal suture; prefrontals in contact with postnasals; central gular scales enlarged, longitudinal in arrangement; GAB 83-134 (108.6); PV 26-51 (37.1); PV/GAB 0.27-0.42 (0.34); GOR 174-243 (203.6) for males, 171-255 (205.1) for females; GAB/GOR 0.44-0.65 (0.54); SAT 20-24 (21.2); total preanal scales 5-9 (6.8); terminal preanal scales 1-3 (2.0); one row of enlarged prebrachials; one or two rows of enlarged postbrachials; enlarged preantebrachials in two rows or two rows proximally and one row distally; prefemoral scales enlarged, four (usually) or three rows proximally reducing to three (usually) or two rows distally; infratibials enlarged, in two rows; femoral pores 30-41 (35.0) for males, 26-36 (32.7) for females; subdigital lamellae 24-33 (28.6); longitudinal rows of ventral scutes 27-32 (30.0); transverse rows of ventral scutes 8-10 (8.1). For details of scutellation see figure 26.

Color and Pattern in Alcohol.—Descriptions of specimens in preservative have been presented by Stuart (1942) and Smith and Laufe (1946). Juvenile males possess a broad middorsal field bounded laterally by narrow, white dorsolateral stripes which originate just behind the eye and extend well onto the tail. Between the blue-gray or gray-brown middorsal pigment and the dorsolateral light stripes there are often secondary stripes, velvet black in color, which extend from the occiput to the

base of the tail. The medial border of the secondary stripe is irregular. The middorsal field may be flecked with black or be nearly uniform in coloration. A white ventrolateral light stripe, which may be complete or interrupted, extends from the posterodorsal corner of the ear to the groin, beginning again behind the leg and terminating on the tail. A white postfemoral stripe is continuous with the ventrolateral light stripe behind the leg. The black dorsolateral dark field is prominent and contains faint, light-colored blotches or bars. The ventrolateral field contains white mottling or bars on a black background. The same pattern is evident on dorsal surfaces of the limbs, but the mottling is more pronounced. Ventral surfaces are cream or white in color.

Juvenile females resemble juvenile males except that there are no light-colored blotches or bars in the dorsolateral dark field and the ventrolateral and limb mottling is less well developed.

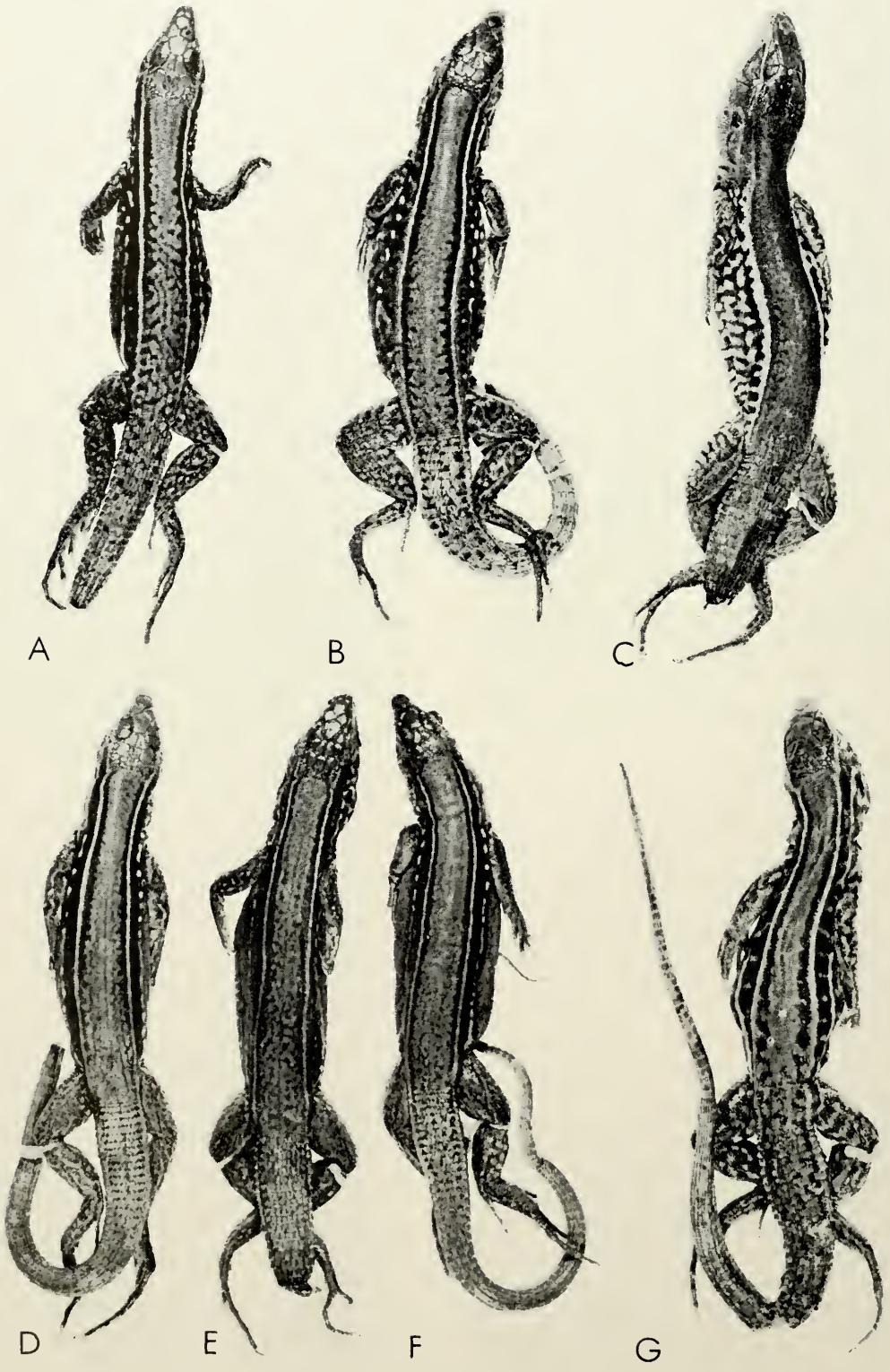
Through ontogeny (Fig. 27) the light ventrolateral and dorsal limb mottling or barring becomes much more pronounced and the ventrolateral light stripe becomes interrupted such that it merges with the ventrolateral mottling. The dorsolateral blotches become white or blue-white in color and fuse with the dorsolateral light stripe in males, giving that stripe an irregular ventral border. Adult females resemble juveniles of both sexes in color and pattern, apparent ontogenetic changes being slight.

Color and Pattern in Life.—There are no descriptions of the coloration of living *Ameiva chaitzami*, although Stuart's (1942) description of the holotype may have been written before extensive fading had occurred in preservative. He stated that the middorsal field and top of the head are olive-brown and that the legs and arms are olive-brown above with black and bluish-white mottling. The anterior surfaces of the thighs are said to be black with blue spots, the venter bluish and the head blue mottled with black. There is no mention of yellow or red pigment in the gular region of this species, the only Middle American *Ameiva* with which I have had no field experience.

Geographic Variation.—The following characters show no significant differences among sample means: Femoral pores of males, number of supralabials, number of infralabials, number of terminal preanals, number of transverse rows of ventral scutes, SAT and COF, COP and SO-SC values.

The three samples of *Ameiva chaitzami* (Fig. 25) were collected in eastern Chiapas, México (Sample 1), western Guatemala (2) and central to eastern Guatemala (3). Samples 1 and 2 are much closer geographically than either is to sample 3 and sample 1 lies slightly northwest of sample 2. This geographic arrangement is reflected in the results of STP analysis of characters which show significant differences among means. Five characters show samples 1 and 2 as constituting one subset, sample 3 a second subset significantly different from the first. These five characters are numbers of loreals and subdigital lamellae, GAB/GOR, numbers of longitudinal rows of ventrals and total preanal scales. For two characters, GAB and PV/GAB, samples 2 and 3 form a subset distinct from that containing only sample 1. For both PV and GOR of females, all three sample means fall into separate, significantly distinct subsets. This is true of samples 1 and 2 for number of femoral pores of females and GOR of males; sample 3 is too small for inclusion in STP analysis. Only for one character, number of supraoculars, is there overlap of sample means: there is a gradient from sample 3 through sample 2 to sample 1, samples 3 and 2 constituting one subset and samples 2 and 1 another.

Because of the inadequate number of samples and the geographic localities from which the samples were drawn,


A
B
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G

detection of clinal trends must await accumulation of additional large samples as the range of the species becomes more fully known.

There seems to be no notable geographic variation in color, pattern or arrangement of gular scales among the three available samples. A comparison of color patterns of equal-sized (68 mm) males from samples 1 and 3 may be seen in Figure 27 (B and G, respectively).

Ecological Notes.—Stuart (1942; personal communication) provided the only insight into the ecology of *Ameiva chaitzami.* He is of the opinion that the species is restricted to pine savannas on the lowlands of central Guatemala where its population density may be kept at a low level by regular burning-off of ground cover. The species is found with *Ameiva undulata,* but never with *Cnemidophorus.* Other Middle American species of *Ameiva* are sympatric with species of *Cnemidophorus* over at least part of their range. Stuart (1942) mentioned a *chaitzami* with a SVL of 66 mm having "well formed eggs."

Smith and Laufe (1946) stated that these lizards ". . . probably occur in all the dry, hot valleys of the upper tributaries of the Río Grijalva in the interior of Chiapas and of western central Guatemala."

Remarks.—Less is known about the biology of *Ameiva chaitzami* than of any other Middle American *Ameiva.* The overall range of the species has yet to be defined.

The divided interparietal (median parietal), which was used by Stuart (1942) to diagnose *Ameiva chaitzami,* is a variable character found throughout the genus in Middle America with varying frequency (Echternacht, 1970). Likewise, I have found the lateral enlargement of the gular scales cited by Smith and Laufe (1946) to be an unreliable character. Color pattern and size remain the most useful characters for distinguishing this probable sibling species from its closest relative, *undulata.*

DISCUSSION

INTRASPECIFIC RELATIONSHIPS

In my opinion the *Ameiva* of Middle America belong to three natural groups the relationships of which will remain obscure until their affinities with South American representatives of the genus are known. The three groups contain one, two and three species (Fig. 28).

FIG. 27. Ontogenetic change in pattern of *Ameiva chaitzami.* A-D and F, UMMZ 94905, E, UMMZ 94901, all from the vicinity of Comitán, Chiapas, México. Field Tag Numbers and SVL are: Males, (A) 473, 45 mm, (B) 482, 68 mm, (C) 461, 73 mm. Females, (D) 483, 55 mm, (E) 365, 68 mm, (F) 501, 75 mm. (G) For comparison, UMMZ 90640, a male paratype 68 mm SVL from along the Cahabón-Languín trail about 2 km N Finca Canihor, Alta Verapaz, Guatemala.

Ameiva ameiva, the only species in Group I, can be distinguished from the others on the basis of a number of scale and pattern characteristics. Chief among these are the presence of five parietal scales, 10-12 enlarged ventral scutes, a large number of scales around the tail, high GAB and GOR counts and a pattern which emphasizes spots instead of stripes in adults. Additionally, *ameiva* is the only species included in the present study having the bulk of its range in South America. The Panamanian portion of that range is but a minor and disjunct part of the whole. Group I is farther removed phylogenetically from Groups II and III than these are from each other.

Group II includes *Ameiva festiva* and *leptophrys.* Both species are essentially lower Central American in dis-

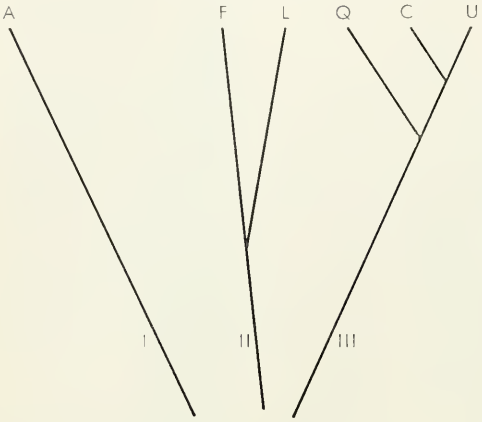

Fig. 28. Relationships of the Middle American species of *Ameiva*. Group I: A, *A. ameiva*. Group II: F, *A. festiva;* L, *A. leptophrys*. Group III: Q, *A. quadrilineata;* C, *A. chaitzami;* U, *A. undulata*. Lengths of the lines and positions of branches do not reflect a time scale.

tribution. *Ameiva festiva* occurs in Colombia, and *leptophrys* is expected there. The group is characterized by the relatively high number of femoral pores and a tendency for the enlarged, posterior scales of the head to become disrupted (Fig. 7). Disruption of head scales is more noticeable in *leptophrys* than in *festiva* but is a more commonly encountered feature of these species than of other Middle American species of *Ameiva*.

Group III consists of *Ameiva quadrilineata, chaitzami* and *undulata*. The group is entirely Middle American in distribution, and is characterized by similarities in pattern and scale characters. The pattern emphasizes stripes, rather than spots, and features a broad, middorsal field without a vertebral stripe. Prefrontal and postnasal scales are in contact. Except for an occasional longitudinal division of the interparietal scale, there is little disruption of posterior scales of the head. *Ameiva chaitzami* is very closely related to *undulata*, from which it is distinguishable primarily on the basis of the color pattern of males. However, the two species are sympatric in central Guatemala. Clarification of the relationships of *chaitzami*, its range and biology remain problems of major importance.

Elucidation of the relationships of the Middle American species of *Ameiva* with those of South America may show that Groups II and III are much more closely related than I have indicated. These may constitute a single group. I should emphasize that these three groups of Middle American *Ameiva* are not the equivalents of the species groups of *Cnemidophorus* established by Burt (1931). Nevertheless, it seems apparent that my Group I would belong to a different species group (*sensu* Burt) than the other species of Middle American *Ameiva*, regardless of whether these other species are found to belong to one or several species groups. The relationships indicated without substantiating comment by Barbour and Noble (1915) are suspect. The taxonomic importance of extensive division of head scales in *Ameiva bridgesi* Cope, *orcesi* Peters and *septemlineata* Duméril and Duméril (Peters, 1964) and the relationships of these species to *leptophrys* and *festiva* require further study. The relationships of *niceforoi* also need clarification (Echternacht, 1970).

INTERSPECIFIC PATTERNS IN GEOGRAPHIC VARIATION

Assessing interspecific trends in variation is considerably more difficult than determining intraspecific trends. This is so for two reasons: 1) The narrow linearity of lowland Middle America virtually dictates that clines will run parallel to the coastlines along a northwest to southeast axis and 2) samples of two or more species from the same locality and of sufficient size for statistical analysis are rarely available. Samples from only ten localities where sympatric occurrence of two or more species was found were large enough for analysis (Table 3), and only three of the six Middle American species of *Ameiva* were present in more than one sample.

TABLE 3.—Localities from which samples of two or more species were available for statistical analysis.

Locality	Species
Costa Rica: Limón: Limón, Los Diamantes and vicinity	*festiva, quadrilineata*
Costa Rica: Limón: Tortuguero	*festiva, quadrilineata*
Costa Rica: Puntarenas: Golfito Region	*festiva, quadrilineata, leptophrys*
Costa Rica: Puntarenas: Osa Peninsula	*festiva, quadrilineata, leptophrys*
Guatemala: El Petén: Piedras Negras	*festiva, undulata*
Honduras: Northern Coastal Localities	*festiva, undulata*
Panama: Bocas del Toro: Almirante and vicinity	*festiva, quadrilineata*
Panama: Canal Zone	*ameiva festiva, leptophrys*
Panama: Isla Escudo de Veraguas	*festiva, quadrilineata*
Panama: Eastern Darién	*festiva, leptophrys*

Ameiva undulata was present with *festiva* in but two samples, and *festiva* was found with *quadrilineata* in two. Although no rigorous statistical analysis was attempted, some parallel trends are evident. For seven characters (infralabials, supraoculars, COP, GAB, GOR, subdigital lamellae and scales around the tail) an increase or decrease in sample mean for *festiva* was paralleled by a like shift in mean for the same character for *undulata* when the two localities of sympatry (Piedras Negras, El Petén, Guatemala, and northern Honduras) were compared. Similar trends were noted for *festiva* and *quadrilineata* for ten characters (GAB, GOR, GAB/GOR, longitudinal rows of ventral scutes, transverse rows of ventral scutes, femoral pores, subdigital lamellae, total preanal scales, terminal preanal scales, and scales around the tail) when stepwise pair comparisons of samples were made between localities beginning with Tortuguero in Costa Rica and running through the Canal Zone to Darién, Panamá, and thence to the Golfito and Osa Peninsula regions of Costa Rica. Perfect agreement was noted only for GOR, but all other characters mentioned showed parallel mean-shifts for at least two-thirds of the possible pair comparisons. Similar parallel changes were noted for *festiva* and *leptophrys* (supralabials, infralabials, COF, COP, transverse rows of ventrals and scales around the tail with COP and COF showing perfect agreement) and *leptophrys* and *quadrilineata* (infralabials and supraoculars). Such parallel shifts in sample means would tend to indicate that these characters are responding in similar ways to environmental differences between sample localities. Considerable additional study will be necessary before any light will be shed on the question of which environmental factors are most important in determining the direction of shift of sample mean for a character from one sample locality to another. Because only increase or decrease in the value of the mean were noted from sample to sample, and not the magnitude of the increase or decrease, it is probable that some shifts are only the result of small sample size and that additional data would show that there has been, in fact, no shift at all.

An important, although likewise unexplained, trend is that of insular populations of *Ameiva* to have higher mean GAB and/or GOR counts than mainland populations (Table 4). Samples are available from Isla Mujeres, Quintana Roo, México *(undulata)*, Isla del Maiz Grande, Zelaya, Nicaragua *(undulata)*, Isla Escudo de Veraguas, Panamá *(festiva, quadrilineata)* and Isla San José, Archipelago de las Perlas, Panamá *(ameiva)*. Samples from the Osa Peninsula, Puntarenas, Costa Rica of *festiva*,

TABLE 4.—Relative positions of island samples with respect to mean Granules Around the Body (GAB) and Granules Occiput to Rump (GOR) when sample means are ordered from largest to smallest.

Species	Total Number of Samples	Relative Position			
		GAB		GOR	
ameiva	7	1		2[a, c]	1[b]
festiva: Isla Escudo de Veraguas	20	1[a]	1[b]	1[a]	1[b]
festiva: Osa Peninsula	20	4[a]	4[b]	15[a]	16[b]
leptophrys	4	2		2	
quadrilineata: Isla Escudo de Veraguas	10	7		5	
quadrilineata: Osa Peninsula	10	1		1	
undulata: Isla Mujeres	45	2		10	
undulata: Isla del Maiz Grande	45	1		2	

[a] Males where sexual dimorphism is evident.
[b] Females where sexual dimorphism is evident.
[c] Tied with sample 3 (See Appendix B) for this position.

leptophrys, and *quadrilineata* also have relatively high dorsal granule counts; the peninsula may be effectively an island as far as *Ameiva* are concerned inasmuch as it is separated from the mainland by a swampy area. It will be obvious from an examination of table 4 that not all insular samples have high dorsal granule counts, but the tendency is evident in a remarkable number of instances. There is no clear relationship between high GAB and GOR counts on the one hand and the ecology of the islands upon which the lizards are living on the other. It would seem that *Ameiva* adapted to life on dry islands would have fewer, but larger, dorsal granules than *Ameiva* of the same size living on wet islands as a selective strategy for prevention of excess water loss. Fewer and larger granules would mean less exposed skin between the granules through which water might be lost than more and fewer scales on animals of equal size. Such an hypothesis is contraindicated by the observation that the islands from which samples of *Ameiva* are available range from very dry (Isla Mujeres) to very wet (Isla Escudo de Veraguas and the Osa Peninsula). It would be instructive to have samples of one species of *Ameiva* from a number of localities for which weather records are available and ranging from relatively dry to relatively wet. Such samples are not presently available and, until they are, this problem is likely to remain unsolved.

Sample mean snout-vent length (SVL) data are not presented in this report because collections are usually strongly biased in favor of large, brightly colored males. The relatively drab juvenile and adult female *Ameiva* are often overlooked by collectors who obtain *Ameiva* incidental to those genera they themselves are working on. A seasonal bias also acts to reduce the numbers of hatchling *Ameiva* in collections in that, in areas having pronounced wet and dry seasons, reproduction may be temporally restricted with hatchlings present only at certain times of the year. Collections made at other times do not include hatchlings. All of the insular samples of *Ameiva* available to me were obtained in June, July, or August, and all are the result of but one or two field trips. With the exception of my own collection from Isla del Maiz Grande, all of these collections were made by individuals primarily interested in other genera. For these reasons, I have little faith in the mean SVL of samples used in this study as an estimate of the true population means. Nevertheless, it is apparent that the insular samples have generally higher mean SVL than main-

TABLE 5.—Correlation between snout-vent length (SVL) and granules around the body (GAB) or granules from occiput to rump (GOR) for five species of Middle American *Ameiva*. Correlation coefficient followed by sample size in parentheses.

	ameiva	*festiva*	*leptophrys*	*quadrilineata*	*undulata*
SVL-GAB Males	0.1101 (112)	0.0897 (243)	0.1345 (101)	−0.0289 (180)	0.1606 (409)
SVL-GAB Females	−0.0403 (133)	0.1531 (233)	−0.1040 (98)	−0.0950 (114)	0.2445 (561)
SVL-GOR Males	0.0737 (114)	0.1857 (268)	——	0.2262 (188)	0.1629 (507)
SVL-GOR Females	−0.0888 (138)	0.0682 (264)	——	−0.2283 (126)	0.1550 (448)

land samples, making it necessary to ask the question whether GAB and GOR counts are in any way correlated with SVL. Correlation analysis was carried out on a species-by-species basis (Table 5). There is no indication that either of the two dorsal granule counts are highly correlated with SVL and the high mean GAB and GOR values of island samples is not an artifact resulting from biased estimates of sample mean SVL.

HISTORY OF *AMEIVA* IN MIDDLE AMERICA

There is no fossil record of macroteiids in Middle America. Therefore, any discussion of the history of *Ameiva* in that region must lean heavily on what is known of present distribution patterns and on geological and faunal summaries relating to Middle America and northern South America. Geological theories concerning Middle America have undergone an evolution of their own over the past 50 years; geological data were summarized by Lloyd (1963), Vinson and Brineman (1963), and Maldonado-Koerdell (1964). Duellman (1966), Savage (1960, 1966) and Stuart (1935, 1951, 1954a, 1954b, 1957, 1964, 1966) provided thoroughly documented discussions of the ecology, origins, and history of the herpetofauna of Middle America, whereas Haffer (1967, 1970) presented an important assessment of the geologic-climatic history of the critical Gulf of Urabá-northwestern Colombia region. Although the following discussion is based in large part on these works, it is a highly speculative and personal view and should be read with that in mind.

Dunn (1931) considered the family Teiidae to be a part of his South American element, having its origins in South America with some genera invading Middle America and one, *Cnemidophorus*, reaching North America. The South American element itself was derived from a generalized tropical American herpetofauna which ranged over much of North and South America during the early Tertiary (Savage, 1960). Subsequent authors have followed this arrangement (Duellman, 1965b; Savage, 1960, 1966; Schmidt, 1943; Stuart, 1957, 1964), although Savage (1966) suggested that the ancestral stock of *Cnemidophorus* was isolated north of the Isthmus of Panamá and that of *Ameiva* south of the Isthmus when the Panamanian portal was open throughout most of the Tertiary. Northward movements of the South American element would have been possible after the closure of the portal in the late Pliocene or early Pleistocene (Lloyd, 1963; Maldonado-Koerdell, 1964). As outlined by Stuart (1957) and Savage (1966, Fig. 23), *Ameiva*, with the exception of *A. ameiva*, probably followed humid, lowland routes from South America into Middle America. Movement through the Pacific lowlands progressed only as far as the Golfito-Palmar-San Isidro del General region of Costa Rica. An Atlantic route was followed northward in México, dispersal to the Pacific lowlands occurring at several points north of what is now Lake Nicaragua. Some

southward movement along the Pacific lowlands of Nicaragua and Costa Rica at a later time is indicated by the present distribution of *A. undulata* (Fig. 17). These routes may have been broader than at present because of lowered sea levels, especially in areas where the continental shelf is extensive (Bennett, 1968).

Of all of the *Ameiva* found in Middle America, *A. ameiva* has made the smallest inroads there. Heatwole (1966) placed its arrival in the Upper Pliocene at the earliest. As an alternative hypothesis, Bennett (1968) suggested that the species dispersed into Panamá during the period of human occupation of Darién. The *A. ameiva* of Panamá resemble those of western Venezuela; Bennett suggested than an open corridor between the two areas for the length of time suggested by Heatwole (over one million years) would have resulted in formation of clines. Subsequent closure of the corridor would have isolated opposite ends of such clines, resulting in morphologically divergent populations. Other than a study emphasizing color pattern (Müller, 1929), no detailed study of the geographic variation of South American *A. ameiva* has been reported. Donoso-Barros (1968) characterized the western population of the species in Venezuela as having a light-colored vertebral stripe. Such a stripe is evident in those *A. ameiva* from eastern Panamá, but lacking in those from the western part of that country (Fig. 4). With the examination of additional samples, remnants of a cline as postulated by Bennett may be found for this and other characters (but see Remarks, p. 19). If remnants of a cline are found, it would indicate that entry of the species into Middle America occurred at a time intermediate to the extremes suggested by Heatwole and Bennett. Recent evidence of alternating dry interglacial and humid glacial periods during the Pleistocene so convincingly presented by Haffer (1967, 1970) would allow for several intervals during which suitable conditions prevailed for the northward movements of *A. ameiva*. Haffer (1970) suggested that the humid forests of glacial times were forced southward during interglacials and during post-Pleistocene dry periods and that central and eastern Panamá, as well as the Gulf of Urabá-lower Río Atrato region of Colombia, were not heavily forested. Thus, it would have been possible for *A. ameiva* to have moved into Panamá prior to the period of human occupancy of the Darién and yet not long enough for establishment of clines. Indeed, if Haffer's scheme is followed, the corridor between central Panamá and Colombia would have been interrupted and reestablished several times, mediating against formation of clinal variation. In any case, it is certain that the Panamanian *A. ameiva* originated from a population of South American *Ameiva* similar to the present population of the species in western Venezuela. Dispersal into Middle America was contained by the availability of non-forested habitats. The species probably reached the islands of the Archipelago de las Perlas at a time when a land connection existed between these islands and the mainland during a period of lowered sea level (Bennett, 1968).

With the exception of *Ameiva ameiva* already discussed, none of the species of *Ameiva* presently inhabiting Middle America would have required a non-forested corridor for northward dispersal. Although the species show a graded dependence upon forested habitat, all are found in or at the edge of forested areas. *Ameiva festiva* and *leptophrys* may, upon completion of studies now in progress, be found to be closely allied to the *A. septemlineata—bridgesi—orcesi* assemblage of northwestern South America. *Ameiva leptophrys,* with its present range limited to eastern Panamá and the Pacific slopes of western Panamá and southeastern Costa Rica

(Fig. 5) may have evolved (along with several other species of reptiles and amphibians) on insular isolates during the Middle Tertiary (Savage, 1966). This seems possible in view of both the present distribution of the species and its broad sympatry with *festiva*. The apparent absence of populations of *leptophrys* on islands at present is a minor set-back to a theory of insular origin in that suitable habitat may have disappeared from the islands in the relatively recent past, or that further collecting will reveal the presence of the species.

Ameiva festiva occurs in both Middle and South America (Fig. 9), as does *A. ameiva*, but *festiva* is continuously distributed over its continental range. Populations of *festiva* on the west and east (or north) slopes of the Andes have diverged markedly in color pattern (Fig. 12). On this basis, the population found in the Chocó of Colombia seems to have diverged relatively early from the ancestral stock. It may possibly have been isolated in the Chocó region during a glacial period during the Pleistocene. Haffer (1967) documented similar isolation in birds and formally proposed the name "Chocó-Refuge" for the area. I have seen no specimens intermediate in pattern between those of the Chocó (Pattern Type C; see page 31 for descriptions of pattern types) and specimens from populations to the north and east. Because of similarity in color pattern of *festiva* from eastern Colombia and those of the San Blas and Golfito-Puerto Armuelles regions of lower Middle America, it seems likely that the latter are derived from the former, rather than from the Chocoan population. The species moved northward, through lowland forests along the Atlantic slopes. The evolution of Pattern Type A probably occurred *in situ* as a result of environmental selection pressures. The present distribution of *festiva* in Middle America is limited to lowland forests. Expansion of its range in northern parts of the region has been prevented by lack of suitable habitat and possibly by competition from *Ameiva undulata* and *Cnemidophorus*. Such expansion in South America has probably been limited by the lack of suitable habitat in Venezuela and eastern Colombia and possibly by competition from *Ameiva bridgesi* in western Colombia.

The early history of the *Ameiva undulata-quadrilineata-chaitzami* complex in Middle America may have been similar to that of *A. festiva*. Having originated from an unknown South American ancestral stock, the forerunners of the extant species moved into Middle America and along both Atlantic and Pacific routes. Extensive northward movement along the Pacific lowlands was probably prohibited by ecological barriers, possibly the climatic filter barrier illustrated by Savage (1966, Fig. 23). Northward migration along the Atlantic slopes progressed to Nuclear Central America and thence, along two routes, on into what is now México. Presumably, ecological divergence in Costa Rica and adjacent Panamá, associated with exploitation of beach and open-ground habitats, resulted in the southern segment of the basal stock becoming *A. quadrilineata*. The range of this species is now disjunct (Fig. 13), but in the past it probably extended along the Atlantic and Pacific slopes of the Western Sierra (terminology of Bennett, 1968) in Panamá and was joined in the lowlands of the isthmus. This contention is supported by the similarity of samples from opposite slopes in the eastern part of the present range of the species, a similarity not found between samples from opposite slopes farther west. Populations of *quadrilineata* on Isla del Caño, Costa Rica, and Isla de Cébaco and Isla Escudo de Veraguas, Panamá, apparently owe their presence to past land connections with the mainland during the Pleistocene (Bennett, 1968).

Ameiva undulata, which continued

to inhabit more forested areas than *quadrilineata*, migrated northward to fill its present range (Fig. 17). Smith and Laufe (1946), having to rely on Schuchert (1935) for geological background, discussed the subsequent history of the species. They postulated a broad distribution of *undulata* in Middle America during the Miocene, with four secondary centers of dispersal, two on either side of the Isthmus of Tehuantepec (Smith and Laufe, 1946, Fig. 4A). Further differentiation was promoted by the opening of the Tehuantepec portal during the Upper Miocene and Lower Pliocene and by subsequent migration, isolation or ecological divergence of populations. If we accept the South American origin of the family Teiidae (Dunn, 1931), and the timing of the reconnection of Middle and South America at the Isthmus of Panamá as Early Pliocene (Lloyd, 1963; Maldonado-Koerdell, 1964), we must reject the hypothesis of Smith and Laufe and can eliminate from consideration the presence or absence of an open portal at the Isthmus of Tehuantepec. It seems probable that one line of *undulata* stock moved through Nuclear Central America along the southern lowlands, crossing to the Atlantic lowlands through the Isthmus of Tehuantepec depression. Movement along the Pacific slopes was limited by xeric conditions to the north. Similar conditions in northeastern México prevented further northward migration on the Atlantic slopes. Eastward migration along the Atlantic lowlands from the Isthmus of Tehuantepec may have been blocked by unsuitable ecological conditions in the form of swamps, or by competition from a second line of *undulata* stock that had migrated along the Atlantic lowlands of Nuclear Central America to reach Guatemala and the Yucatán Peninsula. This second line would have given rise to the extant populations of *undulata* on Isla de Cozumel off the Yucatán Peninsula and on Islas del Maiz east of Nicaragua when these islands were connected with the mainland. Migration of the ancestral stock southward from Nuclear Central America into what is now Costa Rica would account for the present populations along the southern Pacific slopes and on the Meseta Central of Costa Rica. I have postulated that the first of the two lines gave rise to those populations having individuals with color patterns emphasizing stripes or combinations of stripes and lateral bars or blotches. The second line gave rise to those subpopulations characterized by having barred flanks.

Ameiva chaitzami apparently evolved rather recently from a striped form of *undulata*, possibly because of ecological isolation in the arid valley of the Río Grijalva and its tributaries. If further samples linking populations of *chaitzami* with *undulata* are found, it is possible that study will show that *chaitzami* is a form of *undulata*, as inadvertently proposed by Smith and Laufe (1946) and that the sympatry of the two seen today in Guatemala is the result of secondary contact.

Although I think it unlikely, studies of South American *Ameiva* may show that I have underestimated, rather than overestimated, the amount of divergence of the *undulata* complex from other species. If so, this complex, like *Cnemidophorus*, may be found to have its center of radiation in northern Middle America and may be considered a component of the Middle American herpetofaunal element (= "Hanging Relicts," Schmidt, 1943; "Autochthonous Middle American Element," Stuart, 1950) proposed by Savage (1966). Such an arrangement would mean that the complex was isolated in Middle America with the opening of the Panamanian portal and, with some adjustments in timing, would support the hypothesis of Smith and Laufe (1946) concerning evolution of *Ameiva undulata* itself in Middle America.

SUMMARY

The genus *Ameiva* is broadly distributed in Middle and South America, as well as on islands throughout the Caribbean. The genus is represented in Middle America by six species: *Ameiva ameiva* (Linnaeus), *leptophrys* (Cope), *festiva* (Lichtenstein and Von Martens), *quadrilineata* (Hallowell), *undulata* (Wiegmann) and *chaitzami* Stuart. These species are variously distributed throughout the lowland tropics of Middle America from Nayarit and central Tamaulipas, México, through Panamá. *Ameiva ameiva* and *festiva*, and possibly *leptophrys* occur in South America as well. Insular populations are known of all species, except *leptophrys* and *chaitzami*.

Geographic variation is extensive in scutellation and, in some species, color pattern. Sexual dimorphism and ontogenetic change in color pattern is pronounced in some species. Certain characters, such as total number of supralabials, number of dorsal granules from occiput to rump and scales around the tail, are sexually dimorphic in some species, not in others. On the other hand, several characters show no sexual dimorphism at all. Ontogenetic changes are most striking among males. Males of some species undergo marked changes in ventral coloration, especially in the gular region; these may be associated with reproductive state. Clines are apparent in a great many characters and, as might be expected in the context of the essential linearity of the Middle American land mass, most clines run parallel to the coastlines. This is best illustrated by *undulata*, the species having the greatest range in Middle America and for which the most samples were available. In this species, the number of granules around the body and the number from occiput to rump proved the most sensitive indicators of differences between adjacent samples. These two characters are relatively highly correlated. The numbers and arrangement of posterior head scales and of supraoculars were found to be unstable. The former is especially true of *leptophrys* and, to a lesser extent, *festiva*. The condition of a longitudinally divided interparietal, occasionally used to diagnose some species of *Ameiva*, was found to be of wide occurrence in several species.

In Middle America, the species of *Ameiva* run an ecological gamut from the savanna-dwelling *ameiva* to *festiva*, which inhabits lowland tropical rain forest. In the presence of *Cnemidophorus*, *Ameiva* tend toward less open habitats, although the same species may show more latitude in habitat choice if *Cnemidophorus* is absent. As many as three species of *Ameiva* occur sympatrically in lower Central America. Competition among them is partially averted by partitioning of the available habitat. Typically, one species is a forest-dweller, another inhabits open areas and the third is intermediate. Size differences are also important in this context, and partitioning by subadults may be different than that by adults. Little is known of the demography of the Middle American *Ameiva*. All are bisexual.

The species of *Ameiva* of Middle America have been assigned to three groups. These groups cannot be given formal taxonomic recognition until their relationships with South American species of *Ameiva* have been ascertained. The composition of the groups may have to be modified when these relationships are better understood. Group I contains only *Ameiva ameiva*. This group has diverged considerably from Groups II and III, and can be distinguished on the basis of a large number of characters of scutellation and color pattern. The group is primarily South American in distribution. Group II consists of *festiva* and *leptophrys*, both of

which have ranges centered in lower Central America. These two species have in common such characters as a high number of femoral pores and a tendency for the posterior head scales to be disrupted. Group III is made up of *undulata, quadrilineata* and *chaitzami* and is entirely Middle American in distribution. The group is characterized by certain details of scutellation and, especially, color pattern.

The genus *Ameiva* is thought to have originated in South America and to have invaded Middle America following closure of the Panamanian portal in Early Pliocene. Of the Middle American species, *Ameiva ameiva* now occupies a disjunct range in central and western Panamá and in South America east of the Andes. *Ameiva festiva* occurs on eastern and western sides of the Andes; it is thought that the eastern population gave rise to the Middle American population. The species presently has a continuous range along the Atlantic lowlands to Tabasco, México, and along Pacific slopes to southeastern Costa Rica. Based on present distribution, *leptophrys* may have evolved as an insular isolate in the Panamanian portal. *Ameiva quadrilineata* is thought to be a lower Central American derivative of early *undulata* stock, and *chaitzami* a recently evolved offshoot of a striped form of *undulata.* Forerunners of *undulata* itself are thought to have migrated northward on either side of Nuclear Central America. Those moving along the Pacific routes gave rise to the populations in which striped, barred and blotched patterns are emphasized. Those moving through the Atlantic lowlands have given rise to those populations in which lateral bars are emphasized. Populations of *undulata* from the Atlantic lowlands of México between central Tamaulipas and Campeche are derivatives of the line which moved along the Pacific routes and crossed to the Atlantic slopes through the depression at the Isthmus of Tehuantepec. Without exception, insular populations of *Ameiva* in Middle America occur on islands of the continental shelf. These populations were isolated from mainland populations when rising sea levels severed connections with the mainland during the Pleistocene.

The genus *Ameiva* is the most wide-ranging of the exclusively terrestrial Neotropical lizards. Over its entire range, the genus has exploited a broad spectrum of available habitats. For these reasons, a better understanding of the ecological relationships of *Ameiva* may lead to a better understanding of tropical vertebrates in general. To date, very little ecological research has dealt with *Ameiva.* Interesting problems include the relationships of characters of scutellation and color pattern to environmental parameters, the cause(s) and significance of color changes in adult males, and the ecological relationships of sympatric species of *Ameiva* and *Cnemidophorus,* regardless of whether or not these two genera are shown to be congeners. Taxonomic problems of importance to complete understanding of the Middle American *Ameiva* include elucidation of their relationships with South American species (and the relationships of the South American species to one another), the relationships of *chaitzami* to *undulata,* and the status of the population of *undulata* on the Meseta Central of Costa Rica. These are but a few suggestions for future lines of research. There seem to be sufficient problems to keep a number of investigators occupied for years to come.

RESUMEN

El género *Ameiva* está ampliamente distribuido tanto por América Media y Sur America, como por las islas del Caribe. El género está representado en América Media por seis especies: *Ameiva ameiva* (Linnaeus), *leptophrys*

(Cope), *festiva* (Lichtenstein y Von Martens), *quadrilineata* (Hallowell), y *chaitzami* Stuart. Estas especies se encuentran variablemente distribuidas al través de las tierras bajas tropicales de América Media, desde Nayarit y Tamaulipas central, México, hasta Panamá. *Ameiva ameiva* y *festiva*, y posiblemente *leptophrys* ocurren también en Sur América. Se conocen poblaciones insulares de todas las especies excepto de *leptophrys* y *chaitzami*.

La variación geográfica de la escutelación y, en algunas especies, el patrón de coloración es amplia. El dimorfismo sexual y el cambio ontogenético del patrón de coloración es pronunciado en algunas especies. Ciertos caracteres, como el número total de supralabiales, número de gránulos dorsales, desde el occipito a la anca, y las escamas alrededor de la cola, son sexualmente dimórficos en algunas especies pero no en otras. Por otro lado, algunos caracteres no presentan dimorfismo sexual del todo. Los cambios ontogenéticos son más sorprendentes en los machos. Los machos de algunas especies sufren cambios marcados en la coloración ventral, aspecialmente en la región gular, y estos se pueden asociar con el estado de reproducción. Gradaciones son aparentes en muchos caracteres y en su mayoría, corren paralelas a las lineas costera, como se puede esperar del contexto del arreglo linear de la masa terrestre de la América Media. Esto puede ser ilustrado mejor con *undulata*, la especie que tiene la extensión más larga por América Media y de la cual se tienen el mayor número de muestras. En esta especie, el número de gránulos alrededor del cuerpo, y el número desde el occipito a la anca probaron ser los más sensibles indicadores de diferencias entre muestras adjacentes. Estos dos caracteres están relativemente muy correlacionados. El número y arreglo de las escamas supraoculares y las posteriores a la cabeza es inestable. Lo primero es especialmente cierto en *leptophrys* y, en menor grado, *festiva*. La condición de poseer la escama interparietal dividida longitudinalmente, empleada ocacionalmente en las diagnosis de algunas especies de *Ameiva*, fue encontrado siendo de gran ocurrencia en varias especies.

En la América Media, las especies de *Ameiva* pasan por una gama ecologica desde la *ameiva* que vive en las sabanas hasta la *festiva* que habita en las tierras bajas del bosque tropical lluvioso. En presencia de *Cnemidophorus*, *Ameiva* tiende a vivir en habitats menos abiertos, aunque la misma especie puede presentar mayor latitud en la escogencia del habitat si *Cnemidophorus* está ausente. Hasta tres especies de *Ameiva* ocurren simpatricamente en la baja Centro America. La competencia entre ellas se previene por medio de repartimiento del habitat utilizable. Tipicamente, una especie habita el bosque, otra habita las areas abiertas y la tercera es intermedia. Las diferencias en tamano también son importantes en este contexto, y la reparticion del habitat por los subadultos puede ser diferente de la de los adultos. Se sabe muy poco sobre la demografia de *Ameiva* de América Media. Todas son bisexuales.

Las especies de *Ameiva* de América Media han sido asignadas a tres grupos. A estos grupos no se les puede dar reconocimiento taxonomico formal hasta que sus relaciones con las especies de *Ameiva* de Sur América se determinen. La composición de los grupos podrá tener que modificarse cuando estas relaciones se comprendan mejor. El grupo I contiene sólo a *Ameiva ameiva*. Este grupo se ha apartado considerablemente de los grupos II y III, ye se puede distinguir en base al gran número de características en la escutelación y patrón de coloración. Este grupo es principalmente suramericano en distribución. El grupo II consiste de *festiva* y *leptophrys*, ambas con distribuciones concentradas en la baja Centro América. Estas dos especies tienen en común

caracteres como un número grande de poros femorales y la tendencia a poseer escamas rotas en la parte posterior de la cabeza. El grupo III se compone de *undulata, quadrilineata* y *chaitzami* y esta distribuido enteramente por América Media. Este grupo esta caracterizado por ciertos detalles de escutelación y, especialmente, el patrón de coloración.

Se creé que el género *Ameiva* se originó en Sur América y que invadió la Améria Media después del cierre del paso panameño en el Plioceno temprano. *Ameiva ameiva* poseé una distribución discontinua en Panamá central y oeste, y en Sur América al este de los Andes. *Ameiva festiva* ocurre en los lados este y oeste do los Andes; se creé que la población del oeste dio origen a la poblacion de América Media. Esta especie ahora tiene una distribución continua a lo largo de las tierras bajas del Atlántico hasta Tabasco, México, y a lo largo del Pacífico hasta el sureste de Costa Rica. Basado en la distribución presente, *leptophrys* pudo haber evolucionado de un aislamiento insular en el paso panameño. Se creé que *quadrilineata* se derivó, en la parte baja de Centro América, de una linea temprana de *undulata* y *chaitzami* evolicionó recientemente de una forma de *undulata* listada. Se creé que los precursores de *undulata* misma emigraron hacia al norte por ambos lados de Centro América unclear. Esos que tomaron las rutas del lado del Pacífico dieron origen a las poblaciones en las cuales las listas, barras, y manchas son enfatizadas. Las que se desplazaron por las tierras bajas del Atlántico dieron origen a las poblaciones en las cuales se enfatizan las barras laterales. Las poblaciones de *undulata* de las tierras bajas del Atlántico de México, entre Tamaulipas central y Campeche, son derivadas de la linea que se movió a lo largo de las rutas del Pacífico y que crusaron la depresión del istmo de Tehuantepec para dirigirse a la región Atlántica. Sin excepción, las poblaciones insulares de *Ameiva* en América Media ocurren en islas de la plataforma continental. Estas poblaciones fueron aisladas de las poblaciones del continente cuando los niveles del mar subieron durante el Pleistoceno y separaron las conecciones con tierra firme.

El género *Ameiva* es el más ampliamente distribuido de las lagartijas Neotropicales terrestres. Sobre su total distribución, el género ha expotado un gran espectro de habitats utilizables. Por estas razones, una mejor comprensión de las relaciones ecológicas en *Ameiva* puede llevar a una mejor comprensión de los vertebrados tropicales en general. Hasta esta fecha, muy poca investigación ecológia a tratado sobre *Ameiva*. Problemas interresantes incluyen las relaciones de los caracteres de escutelación y el patrón de coloración con parametros ambientales, la causa(s) y significado de los combios de coloracion en machos adultos, y las relaciones ecológicas entre especies simpátricas de *Ameiva* y *Cnemidophorus,* indiferentemente de presentar o no a los dos géneros como si fuesen congenéricos. Problemas taxonómicos de importancia para completar la comprensión de *Ameiva* de América Media incluyen la aclaración de sus relaciones con las especies de Sur América (y las relaciones de las especies suramericanas entre sí), las relaciones entre *chaitzami* y *undulata,* y la posición relativa o status de *undulata* en la Meseta Central de Costa Rica. Estas son no más que algunas sugerencias para futuras lineas de investigación. Parece haber suficientes problemas para mantener ocupados a un número de investigadores durante varios años.

APPENDIX A

An example of summarized data as used in this report, along with results of Gabriel's Simultaneous Test Procedure analysis for number of femoral pores of Panamanian *Ameiva ameiva*. For a complete set of the statistical results of this study, order NAPS Document #01660 from CCM Information Corporation, 866 3rd Avenue, New York, New York 10022; remitting $2.00 for microfiche or $7.00 for photocopies.

Ameiva ameiva: Femoral Pores

Sample Number	$\overline{X}$	Standard Deviation	Sample Size	Range	STP
6	35.0	2.76	23	29-40	
5	34.1	1.64	11	31-36	
7	32.4	1.85	20	29-37	
3	32.3	2.07	24	28-36	
2	31.8	1.93	21	29-35	
1	31.7	2.61	40	25-38	
4	30.1	1.28	13	27-32	
All	32.4	2.69	270	25-41	

APPENDIX B

Specimens Examined

Ameiva ameiva

Sample 1. PANAMÁ: *Canal Zone:* Ancon, MCZ 19805-11, UMMZ 98415-16, 98418; Balboa, AMNH 37129, FMNH 13441, UMMZ 98411-14; Bruja Point, FMNH 13445; nr Corozal, MCZ 19813; Diablo Heights, UMMZ 98417; 6.4 km E Lacone, KU 62701; Miraflores, FMNH 16584-5. *Panamá:* nr City of Panamá, MCZ 9924-27, 9929-30, 9933-41; Panamá City, El Cangrejo, KU 96742-43; Tapia, AMNH 28005-6, 28008.

Sample 2. PANAMÁ: *Canal Zone:* Gatún, FMNH 16555-57, 16572-74, 16580, 16582-83; Cristobal, FMNH 34163-64. *Colón:* Achioté, KU 76109-18, 96737.

Sample 3. PANAMÁ: *Panamá:* Bejuco, KU 107546; Nuevo Gorgona, AMNH 89925-46; ca 12 km NW San Carlos on road to El Valle, KU 107547.

Sample 4. PANAMÁ: *Panamá:* Archipelago de las Perlas, Isla San José, AMNH 66491, USNM 120611-23.

Sample 5. PANAMÁ: *Herrera:* Las Minas, ANSP 22452; Parita, USNM 127291-94, 127296; 8 km SE Parita, KU 107538-39; Pesé, KU 107540-45.

Sample 6. PANAMÁ: *Los Santos:* Guánico, KU 107521-35; Playa Guánico, near mouth of Río Guánico, KU 107909; Las Palmitas, USNM 148207-11, KU 110731-34.

Sample 7. PANAMÁ: *Panamá:* S Slope Cerro Campana, KU 76094-106, 107548-54.

Additional Specimens Not Used In STP Analysis. COSTA RICA: No definite locality, BMNH 80.6.21.1-2. PANAMÁ: *Canal Zone:* Alajuela, UMMZ 76104(4); Ancón, KU 110740; Bas Obispo, USNM 54129; Camp Chagres, KU 76107-8; Chagres, USNM 5519; Culebra, FMNH 16559-61; Culebra Cut, FMNH 16554; Fort Kobbe, KU 110739; Fort Kobbe, Venado River, KU 110742-43; El Vigia, UMMZ 76012; Frijoles, UMMZ 63760; Gamboa, AMNH 32818; Juan Mina, Chagres River, KU 108258-61; Lower Chagres, AMNH 37073-4, 37077; Madden Dam, UMMZ 76015(2); Madden Forest Preserve, KU 96740-41; Río Abajo, FMNH 130685; Río Frijoles, USNM 8394; Road K9, FMNH 130972; Rosseau, KU 62702; Summit, FMNH 130683, 131309; nr Summit Experimental Gardens, UMMZ 95484; Tabernilla, FMNH 16585-87, USNM 54130. *Chiriquí:* 2.5 km E La Concepción, KU 96736; Remedios, AMNH 28390; 3 km W Río Chorcha, KU 95540-44; 16 km W Río Chorcha, KU 95545; Río Salado, KU 95546-47. *Coclé:* Bank of Río Chico de Natá, KU 95548-52; El Valle, AMNH 89924; 16 km S, 9 km W Penonomé, KU 107536; 19 km S, 9 km W Penonomé, Puerto Posoda, KU 107537. *Colón:* Portobello, USNM 65122; Quebrada Bonita, KU 96738-39; Santa Rosa, AMNH 71705. *Herrera:* Tres Puntas, ANSP 22470-74. *Los Santos:* Jobero, KU 110735-36; Pocri, KU 107520; Punta Mala, AMNH 71704. *Panamá:* Cañitas, UMMZ 124148-50; Cerro Azul, AMNH 89947-48; Chorrera, AMNH 71703, FMNH 57597-98; Flora de Lagunas (Río Cañitas), UMMZ 124146-47; Gatuncillo, UMMZ 76013; Isla San Miguel, MCZ 9942-47; Isla Taboga, FMNH 16576, USNM 54197, 54205, 102754-56; Isla Taboguilla, USNM 102809-10; Juan Díaz, KU 110737-38; Nuevo Emperador, FMNH 130937, 130939-45, KU 110471; Pacora, AMNH 32817, FMNH 120956; Río Bayano, USNM 53980; Río Mamoni, FMNH 16566-68; Río Mamoni, 5 km E Chepo, KU 76119-25; Río Tapia, 24 km E Panamá City, AMNH 42953. *Veraguas:* 26 km W Santiago, KU 95553-55; Soná, USNM 51972-73.

Ameiva chaitzami

Sample 1. MEXICO: *Chiapas:* Comitán, UMMZ 94905(24), 94906(5), 94907.

Sample 2. GUATEMALA: *Huehuetenango:* San Antonio Huista, UMMZ 120192; 1 km N San Antonio Huista, UMMZ 120189, 120190(4), 120191(2); 1 km W San Antonio Huista, UMMZ 120195; 1-2 km W San Antonio Huista, UMMZ 120193(18); 1-2 km E San Antonio Huista, UMMZ 120194(4).

Sample 3. GUATEMALA: *Alta Verapaz:* Languín-Cahabón road, MCZ 52170; On Languín-Cahabón road ca 2 km N Finca Canihor, UMMZ 90638-41, 90643. *El Petén:* 1 km N Poptún, UMMZ 124355; 2 km SW Poptún, UMMZ 124356; 2 km NE Poptún nr source Río San Juan, UMMZ 124357.

Additional Specimens Not Used In STP Analysis. MEXICO: *Chiapas:* La Libertad, MCZ 56007, USNM 137216; La Libertad, nr Río Cuilco where it crosses the Guatemalan border, FMNH 100006, 100712-15; unknown, but probably near La Libertad, FMNH 100716.

Ameiva festiva

Sample 1. GUATEMALA: *El Petén:* Piedras Negras, FMNH 115429-43, USNM 133826-36, UIMNH 11349-62.

Sample 2. GUATEMALA: *Alta Verapaz:* Chinajá, KU 55839, 55849-50, 59566; ca 3 km S Chinajá, KU 55841-48, 55857. *El Petén:* 6 km NNW Chinajá, KU 55836; 11 km NNW Chinajá, KU 55837-38; ca 15 km NW Chinajá, KU 55851-56, 59567-73; Toocog, 15 km SE La Libertad, KU 55840.

Sample 3. GUATEMALA: *Alta Verapaz:*

Finca Chama, UMMZ 91319, 91321(2), 91322(2), 91323(3), 91324(2), 91325(2), 91326(4), 91327, 91328(3), 91329(2), 91330, 91331(8), 91332.

Sample 4. HONDURAS: *Atlantida:* ca 15 km E La Ceiba, mtns above Corozal, JRM 2299, 2418-21, 2439-40, 2466-69; Along Río Cangrejal ca 12 km SSE La Ceiba, KU 101195-97; Tela, Lancetilla, UMMZ 70324(3).

Sample 5. NICARAGUA: *Zelaya:* Bonanza, KU 84870-72, 86039-40, 101201-12; 6 km E Bonanza, KU 101198; On banks of Río Tunkey 4 km E Bonanza, KU 101199-200; Eden Mine, ANSP 2133-35.

Sample 6. NICARAGUA: *Zelaya:* Cukra, AMNH 16587-96; Kanawa, AMNH 16597, 16605-16; Between Cukra and Kanawa, AMNH 16600, 16602-4.

Sample 7. NICARAGUA: *Zelaya:* El Recreo, 16 km W Rama on Río Mico, UCLA 9769-70; El Recreo, S side Río Mico, KU 101874; 16 km above El Recreo on Río Mico, UMMZ 79838(12); 11.2 km above Rama, UMMZ 79840(5), 79841(2); Junctions Río Mico and Río Siquía, UMMZ 79839(4).

Sample 8. NICARAGUA: *Río San Juan:* Tuli Creek, AMNH 16666-74, 16676-700.

Sample 9. COSTA RICA: *Heredia:* Puerto Viejo, KU 67298-309, 91787, 104081-82; UMMZ 125505; 1.5 km N Puerto Viejo, KU 67310-11; 2 km NE Puerto Viejo, KU 95558-68; 3 km S Puerto Viejo, KU 95556-57; ca 12.8 km NE Puerto Viejo along Río Sarapiqui, UMMZ 125506(2); Río Sarapiqui at Puerto Viejo, UMMZ 123582-83; Finca La Selva on Río Puerto Viejo, KU 100683-85.

Sample 10. COSTA RICA: *Cartago:* Turrialba, FMNH 101906, 103107, MCZ 55091-92, 55094, USNM 37737, KU 25633-34, 25636-39, 34783-89, 34826-27, 40552, UMMZ 117492; 5 km SE Turrialba, KU 25174-75; 6.4 km SE Turrialba, KU 34778-79; ca 4 km SW Moravia de Turrialba, KU 67312; 4.8 km W Turrialba, Hacienda Florencia, KU 34790-91.

Sample 11. COSTA RICA: *Limón:* Vicinity of mouth of Río Tortuguero, AMNH 89189-203, 89205-15.

Sample 12. COSTA RICA: *Limón:* Guápiles, MCZ 15335-36; La Lola, KU 34798-801, 34807-13, UMMZ 117493(9); Los Diamantes, FMNH 101250, 101252-54, 101256-59, 101261-63, 101904-5, 101907, KU 25581-86, 25619-32, 34772-76, 34802-6; Puerto Limón, KU 34797; Zent, MCZ 15376-81.

Sample 13. PANAMÁ: *Bocas del Toro:* Almirante, FMNH 154445-48, 154451, MCZ 19785-87, KU 80207-11; 3.2 km NW Almirante, KU 96745-46; 4.8 km NW Almirante, KU 96747; 5.6 km NW Almirante, UU 5162; 9.6 km NW Almirante, KU 96748; 12.8 km NW Almirante, KU 96749-52.

Sample 14. PANAMÁ: *Bocas del Toro:* Isla Escudo de Veraguas, KU 108262-71, UU 5153-54.

Sample 15. PANAMÁ: *Canal Zone:* Barro Colorado Island, AMNH 63401, 89949, FMNH 13342-43, MCZ 20612-13, 28066-67, KU 76126-27, UMMZ 63746-55, 63766, 63779, 124156.

Sample 16. PANAMÁ: *Darién:* Río Mono, ca 5 km above junction with Río Tuíra, KU 96781-84; Río Tuíra at Río Mono, KU 96785-804.

Sample 17. COSTA RICA: *Puntarenas:* Agua Buena, Cañas Gordas, KU 40545-48, 40553-58; Golfito, KU 67313; 2.5 km ESE Piedras Blancas, KU 93978; Río Zapote, 8 km E Palmar Norte, KU 93977, 95569.

Sample 18. COSTA RICA: *Puntarenas:* 3 km NW Rincón de Osa, KU 101487-88; 7.2 km SE Rincón de Osa, KU 101489-90; 9.6 km NW Rincón de Osa, KU 101483-86; 10 km SSE Rincón de Osa, KU 101473-80; 11.7 km SSE Rincón de Osa, KU 101481-82.

Sample 19. COLOMBIA: *Córdoba:* Caño Guarmal, FMNH 165260-66; Upper Río Uré, FMNH 165225, 165227-30, 165748-67, 165769.

Sample 20. COLOMBIA: *Chocó:* Andagoya, USNM 124246; Andagoya-Condoto Area, UMMZ 121463; Condoto, UMMZ 121465(13); Tado, ANSP 26265-66.

Additional Specimens Not Used In STP Analysis. BRITISH HONDURAS: *Cayo:* Valentin, UMMZ 92372; *Stann Creek:* Middlesex, FMNH 4460; *Toledo:* 1.6 km E Swazey Branch of Monkey River, MCZ 71606-7; *District Unknown:* Silk Grass Creek State Forest, FMNH 4459; Bobowina, FMNH 49313-14. COLOMBIA: *Boyaca:* Muzo, MCZ 56233; *Chocó:* Boca de la Raspadura, AMNH 18266-68; El Valle, Bahía Solano, Mutis, USNM 151512; El Valle, Pizarro, USNM 151513-14; Pizarro, FMNH 43816-28; Río San Pado, 1.6 km below Boca de la Raspadura, AMNH 18274; Sierra Bauda, ANSP 25526; Sierra de Darién, ANSP 25527-28; Upper Río San Juan, FMNH 15652-53; *Santander:* El Centro Santander, ANSP 25075, 25427; *Departamento Unknown:* E base Cordillera de Bogotá at extreme limit of llanos, ANSP 24165; "Tambo S. Monica, Atlantic Slope," AMNH 18265; Region of Truando, ANSP 9071. COSTA RICA: *Alajuela:* 3.2 km NE Muelle Canal, UCR 23-26; Isla Bonita, FMNH 103103-6; *Cartago:* nr Peralta, Lake Bonilla, KU 43886-8; nr Peralta, Tunnel Camp, KU 34828, 38825; Reventazón, USNM 37492; Río Pacuare, nr Pacuare, KU 34777; Suiza, FMNH 101251, 101255, KU 25635, 34792; Turrialba, FMNH 101909; 6.4-8.0 km S Turrialba, FMNH 101260; *Guanacaste:* Laguna de Arenál, UCR 232-33, 268-69; Tenorio, KU 34814-24; Tilarán, ANSP 24561; 5 km ENE Tilarán, KU 40551; Troncadero, nr Lake Arenál, KU 40539-40; *Here-*

dia: Barro Colorado, KU 100679-80; Between Puerto Viejo and Cariblanco, KU 40537-38; *Limón:* Bataan, KU 34780-82; Pandora, KU 86573-76, 100681-82; Suretka, MCZ 19777, KU 40541-44, 40559-63; *Puntarenas:* Agua Buena, Cañas Gordas, KU 40549-50; *San José:* San Isidro del General, FMNH 101908, 101910, KU 34793-94; 8 km E San Isidro del General, FMNH 120236; 24-32 km NW San Isidro del General, San Juan Mtns., KU 34795-96; *Province Unknown*: Guayabo, FMNH 6167; Río Frío, USNM 19534-36; Locality Unknown, USNM 30558, 32612-13. GUATEMALA: *Alta Verapaz:* Cubiliquitz, UMMZ 91334, 91335(2), 91336(2); Finca Chamá, MCZ 28452-54, UMMZ 91320(2), 91329, 91331; Panzós, UMMZ 9137; Samazana, UMMZ 91333(4); *El Quiche:* Finca Tesoro, UMMZ 89197(4); *Izabál:* "Babos Pl., Mt. Playita," FMNH 20081, 20109-11; Quiriqua, FMNH 20487-88; *El Petén:* Pacomón, USNM 71394; Poptún-San Luis Road, ca 15 km S Poptún, UMMZ 124359; 12 km S Poptún, UMMZ 124360; 10 km NW Poptún, UMMZ 124361(5); Ramate, USNM 71406, 71817, 71823, 71826-27, 71829-31, 71836; *Locality Unknown:* MNHN 5480. HONDURAS: *Copán:* 19.2 km ENE Copán, JRM 2895, 2897; *Cortes:* Hacienda Santa Ana, San Pedro Sula, FMNH 5067-71; Mtns W of San Pedro Sula, FMNH 5074; *Garcias a Dios:* Río Segovia, USNM 24527-28; *Santa Barbara:* Jarál, FMNH 5073; *Yoro:* Mataderos Mountains, FMNH 21781, MCZ 38924; Portillo Grande, MCZ 38925; Subirana Valley, MCZ 38926; *Departamento Unknown:* Carmelina, USNM 62972; Lake Ticamaya, FMNH 5072. MEXICO: *Chiapas:* Palenque, USNM 133818-25, UIMNH 11343, KU 94107-8; *Tabasco:* Teapa, USNM 47454-56. NICARAGUA: *Río San Juan:* Greytown, USNM 19533-34, 19640-1; *Zelaya:* 3-4 km W Bluefields, KU 101213-15; Cupitna, AMNH 16633-51; Río Escondido 70 km from Bluefields, USNM 19735, 19871. PANAMÁ: *Bocas del Toro:* 11 km NW Almirante, FMNH 68171; Bastimentos, USNM 150021; Boca del Drago, USNM 142332-33; Cayo Agua, USNM 150014-15; Río Cahuita, ca 5 km above mouth, KU 108278-79; Río Changena, FMNH 130971, KU 110744-45; *Canal Zone:* Cerro Azul, FMNH 130684; Cristobal, FMNH 34165; Gamboa, FMNH 131308; Gatún, FMNH 16654-56, USNM 54134; *Chiriquí:* Boquete, UMMZ 58296; El Volcán, USNM 129924; Finca Palosanto 7 km NW El Volcán, Río Chiriquí Viejo, KU 96808-11; Finca Santa Clara, KU 110753-54; Volcán Chiriquí, UMMZ 101787; *Coclé:* El Valle, FMNH 47456; Finca El Valle de Antón, FMNH 60174; *Colón:* Achiote, KU 76129-30; Candelaria Hydrographic Station, FMNH 68172-73; Portobello, FMNH 16652-53, USNM 54072-73, 80044; 3.5 km SE Puerto Pilón, KU 110755; Río Candelaria nr Hydrographic Station, FMNH 68174-76; *Darién:* Caña, USNM 50134, 50136, 50138-39, 50142-43; El Real, KU 80529; Laguna, KU 76131; Río Cupe, ca 12 km SSW Boca de Cupe, KU 96805; Río Esnape, Sambu Valley, MCZ 17224-29; Río Jaqué, 1.5 km above Río Imamado, KU 110751-52; Río Jesuito, Sapo Mtns, MCZ 17179-80, 17189; Río San Antonio nr base of La Jarcia, KU 110750; Tacarcuna, KU 76132-39; Tacarcuna Village, USNM 141819-20; *Panamá:* S Slope Cerro Campana, KU 76128; Cerro Jefe, KU 96806-7; E Slope Cerro Jefe, KU 80530-37; NW Slope Cerro Prominente, KU 80538-39; Chepo, FMNH 16656; El Valle de Antón, trail to La Mesa, FMNH 68177-79; Río Abajo, FMNH 57599; Río Siluganti, UMMZ 124151-55; *San Blas:* Camp Sasardí, KU 110748-49; Camp Summit, KU 110746-47; *Veraguas:* Mouth of Río Concepción, KU 108272-77; *Province Unknown:* Cabima, USNM 48504; Chico, UMMZ 76011; Nombre de Dios, MCZ 26944; Punta de Pena, USNM 38693-98; "Veragua," ZMB 881a, 881b.

Ameiva leptophrys

Sample 1. COSTA RICA: *Puntarenas:* Camp Seattle, 6.4 km inland from Rincón de Osa, USC(CRE) 752; Vicinity of Rincón de Osa, KU 101491-528, 101825.

Sample 2. COSTA RICA: *Puntarenas:* Coto, Golfo Dulce, UMMZ 71999-72002; Esquinas Forest Preserve between Golfito and Palmar, KU 34766-70; 3.2-4.8 km W Palmar Norte on road to Puerto Cortez, USC(CRE) 7101c-7101f; 6 km W Palmar Norte, KU 93982-83, 95570-82; 6 km SE Palmar Norte, KU 67314-16; Río Zapote, 8 km E Palmar Norte, KU 93980-81; Villa Neilly, nr town of Corredor, USC(CRE) 179a; 12.3 km WNW Villa Neilly, KU 67317.

Sample 3. PANAMÁ: *Canal Zone:* Barro Colorado Island, AMNH 47018-19, 63403(2), 89953, ANSP 23021-22, FMNH 13307, 13344-47, 13375-76, MCZ 28063-65, 29386, KU 76140-45, 80540, UMMZ 63756-59, 63780; nr Corozal, MCZ 19814; Corozal Hill, USNM 102743.

Sample 4. PANAMÁ: *Darién:* Río Chucunaque, ca 7 km above Río Mortí, KU 107561-63; Río Cupe, ca 12 km SSW Boca de Cupe, KU 96815; Río Tuíra at Río Mono, KU 96816-25; Río Ucurganti, ca 7 km above mouth, KU 107564-65; Tacarcuna, KU 76158-61; Tacarcuna Village, USNM 141817-18; Three-Falls Creek, AMNH 37870.

Additional Specimens Not Used In STP Analysis. COSTA RICA: *Puntarenas:* Parrita, La Julieta, Finca La Ligia, USC(CRE) 8256, 8260b-8260c; 2.5 km ESE Piedras Blancas, KU 93979; Rincón de Osa, RDS 1122-23, 1170, 1177; *San José:* San Isidro del General, FMNH 103111, 103117, KU 25640-42; *Prov-*

ince Unknown: Pozo Azul de Parris, ANSP 21470; Santo Domingo de San Mateo, USNM 37754. PANAMÁ: *Canal Zone:* Alajuela, UMMZ 76009; Camp Chagres, KU 76146-48; Corozal, AMNH 67073; Gatún, USNM 54142; 0.5 km S Juan Mina, FMNH 68159; Madden Dam, UMMZ 76010; Miraflores, FMNH 16650; Río Cardenas, Corozal, USNM 53868; *Chiriquí:* Progreso, MCZ 19865; 13 km N Puerto Armuelles, KU 96814; *Coclé:* El Valle, AMNH 89950-52, USNM 129906, KU 76162-63; *Colón:* Achiote, KU 76149-51; Portobello, USNM 92593; Quebrado Bonita nr Buenavista, KU 96812; 1 km W Río Piedras, KU 96813; San Blas Point, AMNH 71706; *Darién:* Cana, USNM 50135, 50137, 50140-41; Canclones, UMMZ 124975; nr mouth of Río Canclones, UMMZ 124974; Jaqué, KU 110767-68; Laguna, KU 76156-57; Mt. Sapo, ANSP 22963, MCZ 17201-3; Río Jaqué, 1.5 km above Río Imamodo, KU 110769-70; Río Jesuito, Sapo Mtns, MCZ 17196-97, 17199; *Herrera:* Las Minas, ANSP 22450; *Los Santos:* N Slope Cerro Cambutal, KU 107555-56; Guánico Abajo, KU 110771; *Panamá:* Cerro Azul, USNM 54136, 54147; Cliffs W of Cerro Campana, FMNH 60178-79; S Slope Cerro Campana, KU 76152-53, 107558-59; Chepo, FMNH 16645; Las Cumbres, KU 96827; Nuevo Emperador, FMNH 130938; nr Panama City, MCZ 10925, 10927; 2.8 km ENE Panama City, Río Pacora, KU 96826; 9 km NNE Pacora, Río Pacora, KU 107557; Río Mamoni, 5 km E Chepo, KU 76154-55; Río Siluganti, UMMZ 124144-45; Río Tocumen, MCZ 19816; *San Blas:* Camp Sasardí, KU 110756-65; Camp Summit, KU 110766; *Veraguas:* Mangillo, ANSP 22450.

Ameiva quadrilineata

Sample 1. NICARAGUA: *Río San Juan:* Greytown, USNM 19537-45, 20741-42, 32230; Río San Juan, USNM 24984.

Sample 2. COSTA RICA: *Limón:* Colorado Bar, AMNH 16726-28; Tortuguero, USC(CRE) 2653(2); Vicinity of mouth of Río Tortuguero, AMNH 89217-46.

Sample 3. COSTA RICA: *Limón:* Los Diamantes, UMMZ 117491; La Lola, USC (CRE) 128(3), 8063, 8070(3); Zent, MCZ 15382-85.

Sample 4. PANAMÁ: *Bocas del Toro:* Almirante, FMNH 60171-72; Careening Cay, KU 96840-44; Cayo Zapatillo Grande, KU 96845-51; Isla Bastimentos, Bastimentos, KU 96831-39; Isla Bastimentos, Punta Vieja, USNM 150016-20, 150022-23; Isla Colón, road from Bocas to la Gruta, KU 96829-30.

Sample 5. PANAMÁ: *Bocas del Toro:* Isla Escudo de Veraguas, KU 108280-85, UU 5166.

Sample 6. COSTA RICA: *San José:* San Isidro del General, FMNH 103115, KU 25643-50, 34685-89, USC(CRE) 2742; 4.8 km NE San Isidro del General, USC(CRE) 2843; 5.4 km SW San Isidro del General, UMMZ 117490(2); 3.2 km W San Isidro del General, KU 25651; 8 km SE San Isidro del General, KU 95583-90.

Sample 7. COSTA RICA: *Puntarenas:* 1.5 km E Palmar Norte, KU 95592-93; 6 km W Palmar Norte, KU 95633-40; 3.2-4.8 km W Palmar Norte on road to Puerto Cortez, USC (CRE) 7101a-7101b; 5 km SE Palmar Sur, KU 67318-19; 6 km SE Palmar Sur, KU 67320-25; Río Zapote, 8 km E Palmar Norte, KU 95607-20, 95622-26, 104083-85.

Sample 8. COSTA RICA: *Puntarenas:* Rincón de Osa, RDS 1136-38, 1144, 1147, 1152, 1154-63, KU 101463-69, USC(CRE) 7239(14); 3 km NW Rincón de Osa, KU 101470-72; 11.7 km SSE Rincón de Osa, KU 101459-62.

Sample 9. PANAMÁ: *Chiriquí:* Comarca del Barú, Puerto Armuelles, FMNH 68166-67, Progreso, UMMZ 58186-202; 8 km S Progreso, KU 96852; Puerto Armuelles, MCZ 45668-71; 13 km N Puerto Armuelles, KU 96853-65.

Sample 10. PANAMÁ: *Chiriquí:* Boquete, ANSP 21941-43, UMMZ 58183-85, 58209-18.

Additional Specimens Not Used In STP Analysis. COSTA RICA: *Limón:* Colorado Bar, AMNH 16729-75; La Fortuna, AMNH 99679; Old Harbor, USNM 32614-16; Suretka, KU 40578; *Puntarenas:* 0.8-1.6 km E Barú along N bank of Río Barú, USC(CRE) 7096; Buenos Aires, FMNH 2519; Isla del Caño, UMMZ 71194; Coto, UMMZ 72005-6; El General (Viejo) between Palmar Sur and Golfito, KU 34690; Esquinas, KU 34691; Golfito, USC(CRE) 7111(5), 7233(3); Km 47 on railway to Golfito, USC(CRE) 176(8), 177 (2), 178; Finca El Helechales, 15 km NE Potrero Grande, USC(CRE) 8268, 8271; 27 km E Palmar Norte, Río Punta Nuevo, KU 95596-606; 30 km E Palmar Norte, Río La Vieja, KU 95627-32; 2-5 km ESE Piedras Blancas, KU 93984-86; Puerto Uvila, UMMZ 72004; Rincón de Osa, RDS 1139-40, 1142, 1145-46, 1148-51, 1153; San Isidro del General, FMNH 103116; 22 km SE San Isidro del General, USC(CRE) 2648; 57 km SE San Isidro del General, KU 95591; Villa Neilly, USC(CRE) 179; 1.6 km E Volcán de Buenos Aires, Cone Finca, UMMZ 117573; *San José:* San Isidro del General, 3.2 km W Intabee, FMNH 103102. NICARAGUA: *Río San Juan:* Greytown, USNM 6053(2). PANAMÁ: *Chiriquí:* SW Slope Cerro Hornito, KU 96867; 11 km NE Gualacó Road to Valle Hornito, KU 96866; El Hato, edge of lava flow, FMNH 130686; Llano del Volcán above Paso Ancho, FMNH 60175-77, 68168-70; *Herrera:* Las Minas, ANSP 22454-55; *Veraguas:* 8 km SW El Mariá, KU 107566; Isla Cebaco, KU 96828.

Ameiva undulata

Sample 1. MÉXICO: *Tamaulipas:* Gómez Farías, UMMZ 110802, 110839; nr Gómez Farías, UMMZ 111145; 8 km NE Gómez Farías along Río Sabinas, UMMZ 101476-78, 101479(6), 101480-82, 101515-16, 104059 (7), 105489, 111142-44; Paño Ayuctle, 8 km NE Gómez Farías, UMMZ 98982.

Sample 2. MÉXICO: *San Luis Potosí:* Axtla, AMNH 67341; Huichihuayán, USNM 133859; Tamazunchale, AMNH 66065-7, FMNH 38611, UIMNH 27360, 51207; 3.2 km NE Tamazunchale, TCWC 4090-92, UMMZ 119819, UIMNH 16804; Xilitla Region, KU 24056-7.

Sample 3. MÉXICO: *Veracruz:* Tierra Colorado, FMNH 75793, 126933-41, MCZ 56004.

Sample 4. MÉXICO: *Veracruz:* Cuautlapam, KU 105823, UMMZ 41423-32, 41434-42, 41444-51, 41453-54.

Sample 5. MÉXICO: *Veracruz:* Catemaco, UMMZ 118727; 0.8 km W Laguna de Catemaco, UMMZ 126412; 4 km NE Catemaco, UMMZ 126409; Coyame, UIMNH 36877, 39217-18, UMMZ 111456, 114794; 1 km S Dos Amates, between Sontecomapan and Catemaco, UMMZ 126413; Laguna Encantada, 3 km NE San Andrés Tuxtla, UMMZ 119820, 126407; Rancho El Tular, ca 8 km N San Andrés Tuxtla, UIMNH 39212; San Andrés Tuxtla, USNM 46899-904, UIMNH 24691, 27347, 28054, 28056; nr San Andrés Tuxtla, FMNH 126709; 2 km NE San Andrés Tuxtla, UMMZ 121156; ca 4 km N San Andrés Tuxtla, UIMNH 39212; San Martín Mountains, UIMNH 35460; Sontecomapan, UMMZ 114795, 126408.

Sample 6. MÉXICO: *Veracruz:* Hacienda La Oaxaqueña, AMNH 62331-33; 20 km S Jesús Carranza, KU 23953, 24186; 25 km SE Jesús Carranza, KU 26956-57, 26959, 26962-63, 26965-71; 35 km SE Jesús Carranza, KU 23950; 20 km ENE Jesús Carranza, KU 26955, 26961.

Sample 7. MÉXICO: *Tabasco:* Frontera, USNM 25091, 46659, 47453; 16 km SW Frontera, KU 95669-78.

Sample 8. MÉXICO: *Campeche:* Balchacaj, FMNH 106716-18, 106721, UIMNH 26167-70; Tres Brazos, FMNH 106719, UIMNH 26172-75, UMMZ 81924.

Sample 9. MÉXICO: *Campeche:* Dzilbalchen, KU 75589-98.

Sample 10. MÉXICO: *Yucatán:* Pisté, KU 70598-600, 70604-5, 70609, 70611-15, 70617, 70620-26, 70628-29, 70631-32, 70634-35, 70637-41.

Sample 11. BRITISH HONDURAS: *Cayo:* Central Farm, MCZ 71608-9; El Cayo, UMMZ 75012; 1.6 km NW El Cayo, USNM 71372-73; Xunantunich Ruins, MCZ 71619-21.

Sample 12. GUATEMALA: *El Petén:* Tikal, UMMZ 117875(8), 117876(7); Uaxactún, AMNH 68507-16, 70938-42, UMMZ 70415-19.

Sample 13. GUATEMALA: *El Petén:* Piedras Negras, MCZ 66965, UIMNH 11363-93.

Sample 14. GUATEMALA: *Alta Verapaz:* Canihor, UMMZ 91305(21), 91306(3), 91307 (4), 91308; Pinales, UMMZ 91316.

Sample 15. GUATEMALA: *Progreso:* El Rancho, UMMZ 106994(11), 106995(6); Finca Bucural, UMMZ 107000(9), 107001(4).

Sample 16. HONDURAS: *Copán:* Copán, UMMZ 83035(16).

Sample 17. HONDURAS: *Atlantida:* 1 km W La Ceiba, KU 101227; 2 km SE La Ceiba on Río Cangrejal, KU 101228-38; 8 km SE La Ceiba on Río Cangrejal, KU 101239-42; 12 km SSE La Ceiba on Río Cangrejal, KU 101252; ca 15 km E La Ceiba in mountains above Corozal, JRM 2318, 2441-42, 2460-61, 2470.

Sample 18. HONDURAS: *Yoro:* 0.5 km N Coyoles, JRM 2004-7; 2 km S Coyoles along Río Aguan, KU 101216-26, 101254-59, 107911-14, 109973-74; 5 km E Coyoles, JRM 2082-89; 25 km WSW Coyoles, Rancho San Lorenzo, JRM 2116.

Sample 19. HONDURAS: *Colón:* 0.5 km SW Trujillo, JRM 2554; 1 km SSW Trujillo, KU 101249-51; 0.5-1.5 km W Trujillo, JRM 2511; 1-3 km W Trujillo, KU 101243-47; 2 km E Trujillo, JRM 2533-36; 2 km W Trujillo, KU 101248.

Sample 20. HONDURAS: *Olancho:* 0.5-1.0 km WNW Catacamas, JRM 1433-37; 1 km NW Catacamas, JRM 1551; 1.5 km NW Catacamas, JRM 1554-55; 2-3 km NW Catacamas, JRM 1526-29; 4.5 km SE Catacamas, Esquela Agricola Nacional de Agricultura, JRM 1586-87, 1622, 1628-30; 6.5 km SE Catacamas, JRM 1638-39.

Sample 21. NICARAGUA: *Zelaya:* Isla del Maiz Grande, AMNH 97045-67, 97637, MCZ 26970, 26972, 26974, USNM 94053, KU 85988, 85997, 85999, 101268, 101273-74, 101276-77, 101281-86, 101292, 101299-301, 101305-6, 101309-10.

Sample 22. MÉXICO: *Colima:* Hacienda Paso del Río, FMNH 75794, 126436, 126438-41, 126443-47, 126449-51, 167438, UMMZ 80118(2), 80119; Manzanillo, FMNH 100054; 1.6 km W Pascuales, UMMZ 80113(3); 0.4 km E Pascuales, UMMZ 80114; 6 km SW Tecumán, UMMZ 80110; 8 km SW Tecumán, UMMZ 80111(3), 80112(5), 80120.

Sample 23. MÉXICO: *Colima:* Colima, AMNH 5185, 15448-49; NW of Colima, AMNH 15838-42; 0.8 km SW Colima, AMNH 12634-35; 2.4 km SW Colima, AMNH 12643; 6.4 km SW Colima, KU 29529; near Salvador, MCZ 52172.

Sample 24. MÉXICO: *Guerrero:* Mtns N of Acapulco, FMNH 126351, 126355, UIMNH 27344; 8 km E Coyuca, USNM 133849-53; Between km 431-432, camp nr El Triente, FMNH 126353; 2 km N El Triente, UMMZ 119564; 1.6 km N Organos, S of El Triente, UIMNH 27345; E San Andreas de la Cruz, KU 87417.

Sample 25. MÉXICO: *Guerrero:* Acahuizotla, TCWC 7780, 9587-88, 11320, UMMZ 119563; Agua del Obispo, UMMZ 119565, TCWC 7575, KU 87413-16; nr Agua del Obispo between Rincón and Cajones, FMNH 126352, 126354, MCZ 56005; Mtns near Agua del Obispo, TCWC 7576; 8 km SW Chilpancingo, TCWC 9590; 1.6 km SW Cototlipa, TCWC 9591.

Sample 26. MÉXICO: *Oaxaca:* 6.4 km S Candelaria, KU 38234; Chacalapa, KU 38230-33; 3.2 km W El Soledad, UIMNH 8421-27.

Sample 27. MÉXICO: *Oaxaca:* Tres Cruces, 32 km SW Tehuantepec, UMMZ 81897(2), 81898(3), 81899(2), 81900(3), 81901(5), 81902(4), 81903(5), 81904(6).

Sample 28. MÉXICO: *Oaxaca:* 3.2 km E Tollocito, KU 39722-32, 39734, 44656-57.

Sample 29. MÉXICO: *Oaxaca:* Tapanatepec, AMNH 80002-3, MCZ 27283-300; 2.4 km S, 7.2 km E Tapanatepec, TCWC 17047-48; 4 km W Tapanatepec, KU 59577-80; Río Novillero, 4.3 km W Tapanatepec, UIMNH 39204-8.

Sample 30. MÉXICO: *Chiapas:* Finca San Bartola, ca 19 km SW Cintalapa, UIMNH 8437-41, 39229-41; nr San Ricardo, FMNH 106715, UIMNH 26157.

Sample 31. MÉXICO: *Chiapas:* Abellanal, 2 km SE Florida, TCWC 19764-65; Florida, 50 km E Altimirano, TCWC 19758-63, 19766-86; Las Tazas, 51 km E Altimirano, TCWC 19757.

Sample 33. MÉXICO: *Chiapas:* Esquintla, LACM 9527-28; Distrito Soconusco, 6 km NE Esquintla, UMMZ 86862-71, 86873-88.

Sample 34. MÉXICO: *Chiapas:* Sabana de San Quintín, KU 94109-17, 94119.

Sample 35. GUATEMALA: *Sololá:* Finca Santa Buenaventura, 1 km NW Panajachél, UMMZ 98215(2); Panajachél, MCZ 27515-20, KU 59581, 95653, UMMZ 98201(3), 98214(3); 1 km E Panajachél, KU 95657; 3 km E Panajachél, KU 95654-56; 3 km NE Panajachél, UMMZ 98202; 1 km NW Panajachél, UMMZ 98203(2), 98204; 2 km NE Panajachél, UMMZ 98212; 4 km NE Panajachél, UMMZ 98213; Sololá, UMMZ 98205(2); On road to Sololá, 1 km from Panajachél, UMMZ 98206.

Sample 36. GUATEMALA: *Jutiapa:* Finca La Trinidad, UMMZ 107421, 107422(8), 107423(5), 107424(3), 107425(6), 107427(3), 107428, 107429(3).

Sample 37. GUATEMALA: *Jutiapa:* Hacienda Mongoy, UMMZ 107002(6), 107003, 107004(3); Jutiapa, UMMZ 106997(4), 106998, 106999(16).

Sample 38. EL SALVADOR: *Libertad:* 2 km SE Colón, KU 62608-70; Laguna de Chanmico, UMMZ 117486(2); 0.8 km N, 16 km W La Libertad, TCWC 17059; Rancho Belmar, nr La Libertad, LACM 9370. *San Salvador:* Instituto Tropical, San Salvador, KU 62066-67; 0.4 km NW Instituto Tropical, UMMZ 117487; 0.8 km NW Instituto Tropical, UMMZ 117488; 1.6 km NW San Salvador, KU 42262.

Sample 39. NICARAGUA: *Chinandega:* 4 km N, 2 km W Chichigalpa, KU 86036; Chinandega, MCZ 9540, 9546; Finca San Isidro, 10 km S Chinandega, KU 86030-31; Foothills, N Slope Volcán San Cristobal, KU 86032-35; Hacienda Bellavista, Volcán Casita, KU 101875-77; San Antonio, KU 86008-26.

Sample 40. NICARAGUA: *Matagalpa:* Guasquali, UMMZ 116420(3); Matagalpa, UMMZ 116414, 116418(5); 0.8 km E Matagalpa, UMMZ 116416; 1.6 km W Matagalpa, UMMZ 116417, 116419; 2.4 km E Matagalpa, UMMZ 116415(2).

Sample 41. COSTA RICA: *Guanacaste:* Hacienda Coyolar, 4.8 km N, 4.0 km W Liberia, USC(CRE) 8206(15), 8207(2); Hacienda La Norma, 5 km N, 4.5 km W Liberia on Río Colorado, USC(CRE) 100(2), 103(3), 104, 105(3), 106(8), 107(4), 111, 251.

Sample 42. COSTA RICA: *Guanacaste:* Cañas, USNM 80894; 1.5 km E Cañas, USC(CRE) 208-9; 1 km S Cañas, USC(CRE) 201; 7 km N, 3 km E Cañas, USC(CRE) 270-77; Finca Taboga, 11 km S Cañas, USC(CRE) 631, 7166(2); Río Javillo, 2 km S Las Cañas, USC(CRE), 202-3.

Sample 43. COSTA RICA: *Guanacaste:* On first river N Santa Rosa, KU 40531-36; Road from Silencio to Tilarán, 1.8 km from Tilarán, USC(CRE) 6240; Road from Silencio to Tilarán, 2.6 km from Tilarán, USC(CRE) 6239(2); Tilarán, ANSP 24566-67; Río Santa Rosa drainage 1.2 km by road SW Tilarán, USC(CRE) 7161; 1.6 km SW Tilarán, USC(CRE) 6270; 2 km W Tilarán, USC(CRE) 732; 4.3 km by road NNE Tilarán, USC(CRE) 8082; 4 km ESE Los Angeles de Tilarán, KU 40527-28; 5.8 km from Tilarán on road to Los Angeles, USC(CRE) 6267; Troncadero, Laguna de Arenál, KU 40529-30.

Sample 44. HONDURAS: *Francisco-Morazán:* El Zamorano, Esquela Agricola Panamericana, AMNH 70368, MCZ 49765-67, 10001-3, KU 101260-67; Río Yeguare, AMNH 70369-79; Valley of Río Yeguare S of Tegucigalpa, AMNH 70470-73.

Sample 46. MÉXICO: *Quintana Roo:* Isla Mujeres, USNM 47568-70, 47651, KU 70585-88.

Sample 48. MÉXICO: *Michoacán:* Apatzingán, FMNH 38977-85.

Additional Specimens Not Used In STP Analysis. BRITISH HONDURAS: *Belize:* Ambergris Cay, 3.2 km N San Pedro, MCZ 71611; Belize, USNM 51879-80, 58373-78; *Cayo:* Augustine, Mountain Pine Ridge, MCZ 71622-24; *Corozal:* 0.3 km N Corozal, MCZ 71610; *Orange Walk:* Gallon Jug, MCZ 71612-18; *Stann Creek:* Mango Creek, MCZ 71627-28; 8 km SW Mango Creek, MCZ 71626; 6.4 km S Waha Leaf Creek, MCZ 71625; *Toledo:* 1.6 km W Swazey Bridge, Monkey River, MCZ 71629. COSTA RICA: *Alajuela:* San Mateo, USNM 37491; "Autopista-Alajuela," UCR uncatalogued; *Cartago:* La Carpintera, AMNH 16314, 16316; *Guanacaste:* Bebedero, USC(CRE) 7162; 1.6 km N Guayabo de Bagaces, USC(CRE) 7024; Playa Sámara, outer coast of Nicoya Peninsula, USC(CRE) 8252; Parríta, La Julieta, Finca La Ligia, USC(CRE) 8255(4), 8260, 8262; 1.6 km S Santa Cruz, USC(CRE) 8218; 1.8 km N Santa Cruz, USC(CRE) 8217(2); *Puntarenas:* 4.3 km E Esparta, UCR 547; *San José:* Barrio México, San José, KU 40526. EL SALVADOR: *La Paz:* 3 km E San Rafael Obrajuela, KU 62065; *San Miguel:* San Pedro, MCZ 57081. GUATEMALA: *Guatemala:* El Rosario, FMNH 68708-10; *Izabal:* 1.6 km NE York, KU 59574-75; *San Marcos:* Finca Carolina, MCZ 22144-48, 27301-5; *Santa Rosa:* Finca Las Vinas, UMMZ 107073-74; *Departamento Unknown:* MCZ 5831, 99840-41. HONDURAS: *Colón:* Belfate, AMNH 58607-9; *Comayagua:* La Libertad, MCZ 38923; *Copán:* Hugito, ANSP 22195-98; *Cortes:* E side Lago de Yojoa, KU 67332; Rancho Agua Azul, Lago de Yojoa, MCZ 49964; 3.2 km W San Pedro Sula, MCZ 29387-88; *El Paraíso:* Arenal, 25 km E Jalapa (Nicaragua), UCLA 14759; Valle de Jamastran, AMNH 70333-35; *Francisco-Morazán:* Cantarranas, ANSP 22199-212; *Gracias a Dios:* Tancín, ca 15 km NW Puerto Lempira, JRM 1732, 1752. MÉXICO: *Campeche:* 3.2 km E Barro San Pedro Y Pablo, AMNH 88877; Champotón, UMMZ 72956-57; *Chiapas:* 3.2 km E El Real, KU 43663-64; Palenque, MCZ 66966; Across Río Usumacinta from Piedras Negras (Guatemala), USNM 108600; San Juanita, Palenque, USNM 108601; *Colima:* Quesería, UMMZ 80109; nr Quesería, FMNH 126437, 126442, 126448; *Guerrero:* nr Rincón, FMNH 100080; *Oaxaca:* La Concepción, nr Tehuantepec, AMNH 66932; Cosolapa, USNM 133920; Juquila Mixes, AMNH 89761-65; Mitla, AMNH 91023-24; 9.6 km N Putla, UIMNH 52952-53; Río Cacahuatepec, UIMNH 52950; Río Canoa, 26 km W Pinotepec Nacional, UIMNH 52951; Sta. Lucía, Tehuantepec, AMNH 65077-78, 65085; Tehuantepec, USNM 30163; Zacatepec, UIMNH 52948-49; *Puebla:* Necapa, Río Necapa, AMNH 76441-43; nr Vegas de Xuchíl, AMNH 58217; *Quintana Roo:* 8 km inland from Vigia, Ascensión Bay, UMMZ 78586; *San Luis Potosí:* Ciudad Maiz, FMNH 126942; nr Cuidad Maiz, FMNH 126946; Palictla, AMNH 67358; 8 km S Valles, FMNH 126947; *Tabasco:* La Venta, USNM 117350; *Tamaulipas:* S of Antiguo Morelos, FMNH 126944-45; Hacienda La Clementina, FMNH 126943, 126948, MCZ 56006, USNM 106141-42; Rancho Santa Ana, 12.8 km E Padilla, MCZ 43634; Río Guayalejo, nr Magiscatzín, MCZ 45557, UMMZ 88232; 11 km W Victoria, FMNH 100050; *Veracruz:* Jalapa, FMNH 126706; Orizaba, USNM 133839; Panuco, MCZ 19255-59; 4 km E Papantla, KU 24189, 24194; San Andrés Tuxtla, FMNH 100020; 16 km WNW Temapache, KU 61791-92; *Yucatán:* Chichén Itzá, MCZ 52171; Culebra Cay, Ascención Bay, UMMZ 78587; Progreso, FMNH 100030; *Estado Unknown:* "Mexico," (Restricted to Tehuantepec, Oaxaca, by Smith, 1940), ZMB 868. NICARAGUA: *Estelí:* Finca Daraili, 5 km N, 14 km E Condega, KU 85984; *Madriz:* 1.6 km SE Yalaguina, TCWC 17051; *Managua:* 12 km E Managua, UCLA 14787; 6.4 km E San Lorenzo, KU 42249; *Río San Juan:* Tuli Creek, AMNH 16675; *Rivas:* within 3 km of Moyogalpa, Isla Ometepe, KU 86029; *Zelaya:* Huaunta Haulover, ANSP 15438-41; *Departamento Unknown:* ANSP 9133-34.

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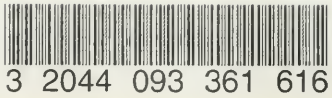
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